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P. 323, 13th line from bottom, for *Rhodendron* read *Rhododendron*.

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No. 1

MAJOR PLANT COMMUNITIES IN A TRANSECT OF THE SIERRA NEVADA MOUNTAINS OF CALIFORNIA

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Among the ecological problems in the Sierra Nevada Mountains of eastern California are the contrasts of physiography, climate, and vegetation on the two sides of the mountains, the differences due to their wide range in altitude, and the interactions between local environments and plant communities. A large amount of information pertaining to these problems is to be found in the works of Jepson ('10, '25), Abrams ('23), Smiley ('15, '21), Merriam ('98), Tidestrom ('25), Shantz ('25), Sampson ('25), Sudworth ('08), Clements ('20), Harshberger ('11), and others. The recent book on the animal life of the Yosemite by Grinnell and Storer ('24) describes conditions in a belt across the Sierra some distance north of the transect here presented, which traverses the middle part of the range.

Some of this region was already known to the writer before beginning, in the spring and summer of 1926, the determination and mapping of the major plant communities in a representative belt transect. This was intended from the outset to constitute a foundation survey on which additional and more detailed investigations might be based.

The location of the transect chosen as typical of the middle Sierra Nevada is shown in figure 1. Except for its west end, it is included in the Sierra National Forest and the Inyo National Forest. Most of it is in Fresno County, although a part of Madera, Mono, and Inyo counties is included. The transect is 7 miles wide and 80 miles long, extending from the floor of the Great Valley on the west to the Owens River Gorge on the east. It is very nearly at right angles to the long axis of the range, and therefore lies in a southwest to northeast position. The country within this strip is considered typical of the middle Sierra Nevada rather than of the southern Sierra.

METHODS

A field map was obtained by marking off the strip on the U. S. Geological Survey topographic sheets¹ of the region and enlarging this four times by

¹ Quadrangles: Lanes Bridge, Friant, Academy, Mariposa, Kaiser, Mount Goddard, Mount Morrison.

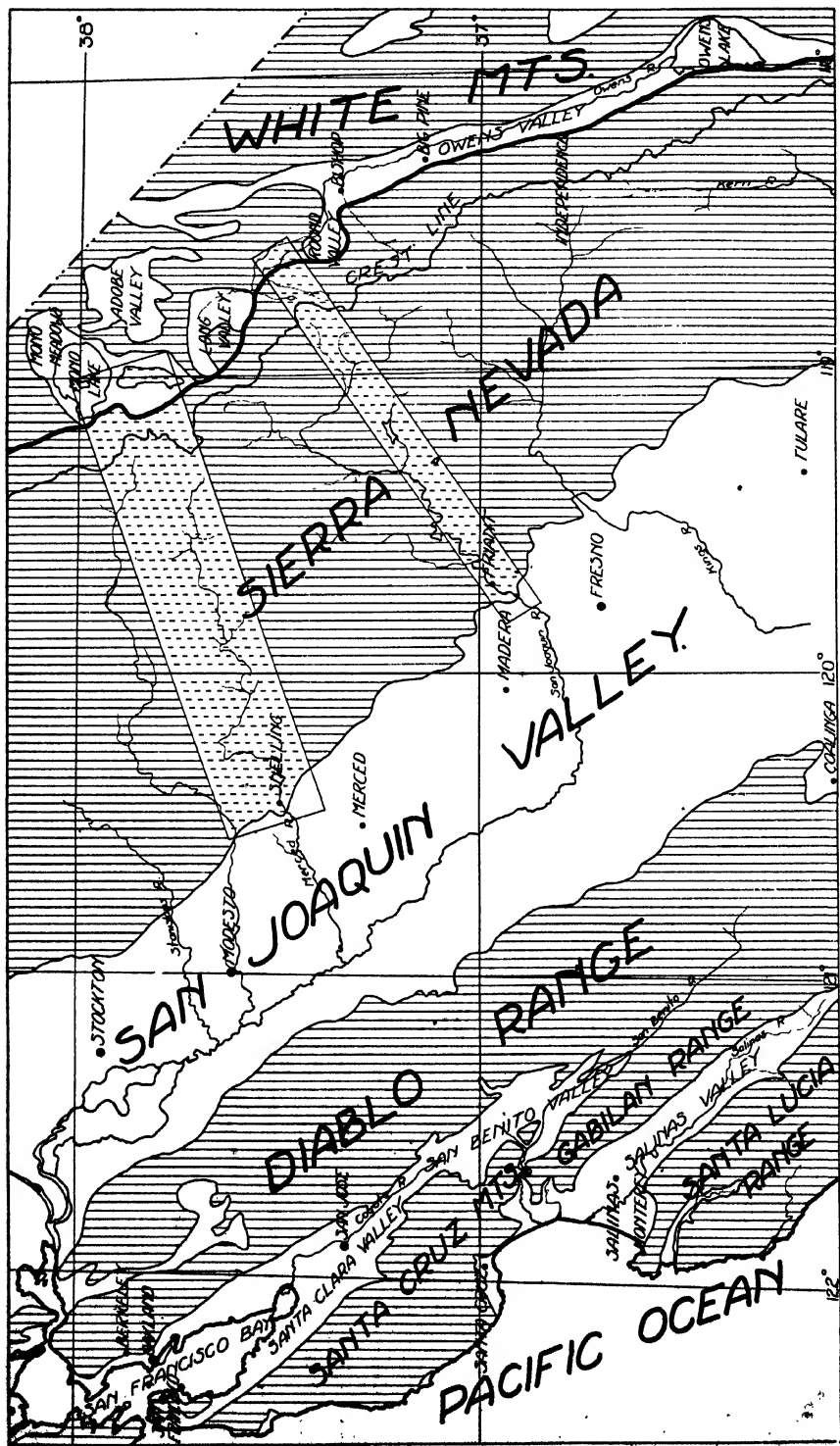


FIG. 1. Physiographic map of middle California, showing location of transects of Grinnell and Storer (upper) and of the present paper (lower). The mountain areas are shaded. The Sierra is distinguished from mountains and valleys to the east by a heavy line representing the eastern base. The crest-line of the Sierra is also shown, not far to the left.

the photostat process. The field work was carried on during June, July, August, and September, 1926, during March and June, 1927, and during short intervals from 1927 to 1930. At this time the vegetation was mapped, field notes were written, specimens were taken and photographs were made. The final map was constructed by tracing the desired features from the field map and supplementing these with other information.

TOPOGRAPHIC FEATURES OF THE TRANSECT

The Sierra Nevada is an immense block of granitic rock overlaid by sediments greatly elevated on the east side by a succession of faultings, producing a very pronounced eastern scarp and a long westward slope of slight and fairly uniform gradient, now submaturely dissected, and glaciated at the higher elevations. The detritus carried by the streams during this process was laid down as extensive sedimentary deposits in the Great Valley. The glacial detritus and great alluvial fans of coarse sediments along the base of the east front are evidences of the same process on the east slope.

The middle Sierra is typical of the range with regard to general topography (Fig. 2). The west slope is deeply dissected by a number of river systems, the most important of which are the Stanislaus, Tuolumne, Merced, San Joaquin, and Kings. In several places the usual topographical aspect of the foothill region, which is in the stage of early maturity, is modified by the presence of lava-capped mesas, such as Table Mountain. A notable feature of the present topography is the presence of a number of artificial lakes, such as Shaver and Huntington lakes. The Sierran crest line attains its greatest average elevation in the southern part of the middle Sierra. In this same region the east front has its greatest height. Farther north, in the region south of Mono Lake, the height of the east front is considerably less because the volcanic deposits originating in the vicinity of Mono Lake are superposed upon the detritus at the base of the range.

A detailed description of the topography of the transect is given at this point. In this description the notable features are considered in the order in which they would be encountered in traveling eastward over the range within the strip.

The floor of the Great Valley in the vicinity of Lanes Bridge is gently undulating, with the courses of the generally westward-flowing ephemeral streams indistinctly defined. Occasional local depressions of undetermined origin and of varying extent and depth occur. These are the so-called "hog wallows." Their importance is here stressed because of the characteristic flora which inhabits them upon the disappearance of the vernal pools that occupy them during the rainy season and late spring. In certain localities the hog-wallow effect occurs on hill slopes. The flood plain of the San Joaquin River cuts across the valley floor at a depth of 50 feet or more below the general level of the country after it emerges from the foothills at Friant.

The stream takes a slightly meandering course near the north side of its flood plain. It is here a braided stream, with many islands in its channel.

The dominant aspect of the lower elevations or "foothills" is that of early maturity. Several mesas occur. The first noticed of these is Little Table Mountain, which rises abruptly for 200 feet on the east and on the west dips gently under the valley floor. A larger and much more extensive one is Table Mountain. This is a basalt-capped mesa, in marked contrast to the conglomerate-capped mesa mentioned above. It rises on an average of about 600 feet above the surrounding country, the basalt stratum dipping southwestward. In the same direction are several smaller mesas and a number of hills with basalt-strewn summits. The lower elevations are marked by several intermittent streams, chief of which are Little Dry Creek and its main tributaries. The other small streams are rather ephemeral. In this part of the transect the river has a canyon of considerable depth, flowing through a gap cut through Table Mountain.

The slopes of the middle elevations within the transect are practically all canyon-sides of the San Joaquin River canyon. This feature is at first not very apparent because of the decreasing gradient as one leaves the river. When viewed from a distance it becomes at once apparent. The canyon of Big Creek forms an eastward extension of the canyon within the strip, the main canyon turning northward out of the strip at the junction of the creek and the river. The Shaver Lake basin, a part of which is in the transect, is the site of an old mountain meadow. It is separated from the river canyon by several low mountain peaks.

The higher elevations east of the range crest are approached by an abrupt rise of over 2,000 feet in a mile at the head of Big Creek canyon to the level of Huntington Lake. At the head of the canyon is a characteristic Sierran dome of large size, Kerckhoff Dome. The Huntington Lake basin is long and narrow, being now almost entirely filled with water. It drops abruptly into Big Creek canyon through several narrow gaps, three of which are now obstructed by concrete dams. The basin is limited from the northwest to the east by Kaiser Crest and Kaiser Ridge and for the remainder by well-rounded ridges with occasional rocky points. A number of important permanent streams flow down these slopes into the lake. The higher elevations of this part of the transect culminate in Kaiser Crest and Kaiser Ridge which, in turn, are dominated by Kaiser Peak (10,300),² an unnamed peak (B. M. 10,643), and Castle Crags (10,367 and 10,614). These ridges, being continuous, describe a wide arc convex northward. They have uniform steep slopes on the southern side. The opposite side drops off in sheer palisade cliffs and crags to the talus in small cirques, and then by more gradual slopes to the canyon of the South Fork of the San Joaquin.

The canyon of the South Fork cuts across the transect almost at right angles, running northwestward. The canyon is wide. The gradient from

² All elevations are given in feet above sea level.

Kaiser Ridge on the west is uniform and steep with a hummocky, glaciated surface closely strewn with low, rounded granite knobs. No corresponding ridge encloses the wide canyon on the east side, though the hummocky surface prevails. In traversing this hummocky country, the river flows alternately through narrow granite trenches and gently sloping meadows. Mono Creek canyon is the larger of two canyons joining that of the South Fork from the east within the strip. It parallels the strip from its lower end, where it widens out before joining the canyon of the South Fork, to the range crest, where it heads in a number of large cirques. The lower end of the canyon is a valley four miles long with an average width of half a mile, Vermilion Valley. Its floor is built of granite-gravel, deposited above a series of more than 25 moraines. At the present time Mono Creek meanders along this valley in large U-shaped curves, while in places it is braided and follows several channels. The canyon of Bear Creek is south of and parallel to Mono Creek canyon. It is smaller than the latter and heads in several cirques on Mono Divide west of the range crest proper. This canyon is similar to that of Mono Creek in having gently sloping meadows at its bottom in places. The south wall of the canyon rises steeply to the top of the Mount Hooper ridge, a part of which is included in the strip. Bear Ridge separates these two canyons. It is a westward extension of Mono Divide with a gradual decrease in elevation westward, and several extensive meadows along its top at the east end. Overlooking these meadows from the northwest is Volcanic Knob (11,153). A little north and between its western end and the South Fork is a small basalt-capped mesa, Giants' Table, which rises 100 feet or more above the surrounding country.

Mono Divide is a spur of the main crest of the Sierra, extending southward for 3 miles, then turning sharply toward the northwest. The slopes toward the west are uniformly steep from its base. Above these slopes rise sharp peaks and jagged spires along the summit. These are the result of glacial sapping on both sides of the divide. The larger cirques, some of which contain small glaciers, are on the eastward side. They drop very steeply into Mono Creek canyon through the First, Second, Third, and Fourth recesses. Opposite the Fourth Recess at the head of Mono Creek canyon lies the very large cirque called Pioneer Basin. It is limited on the north and east by the range crest and on the west by a spur starting from Mount Crocker (12,448) on the crest and terminating above Mono Creek in Mount Hopkins (12,300).

The trend of the crest within the transect between Mount Stanford (12,826) near the north boundary and Mount Abbott (13,736) on the south boundary is nearly north and south with a wide curvature eastward. On the west slope there are still remnants of the ancient peneplain surface which antedates the uplifting. Along both sides of the Crest are large cirques, with precipitous walls, rock slides, talus slopes and moraines.

Beyond the crest the canyon of Rock Creek cuts a deep gash across the east front. The canyon is roughly parallel to the crest line. At its bottom is

the Valley of Little Lakes. The canyon drops rapidly and becomes very narrow before reaching the front of the range. Between this canyon and the crest is the canyon of Hilton Creek, which flows northward out of the strip. The Hilton (Davis) lakes are situated in this canyon near its head. The deep gash in the east slope represented by Rock Creek canyon separates Wheeler Crest from the main part of the range within the strip. Wheeler Crest starts as a spur from the Sierran crest line south of the strip and extends nearly across it. Because of this fact, the very steep eastern slope of Wheeler Crest (11,800) may be said to constitute the east front of the Sierra Nevada within the transect. A long moraine paralleling Wheeler Crest and situated along its western slope forms a basin for the Tamarack Lakes. At the foot of the crest on the east the country rock of the Sierra dips under a great body of alluvial and glacial debris.

The Volcanic Tableland is a recent flow of volcanic material in the region southeast of Mono Lake. Its surface is marked by irregular masses of volcanic rock sculptured into many fantastic shapes. Rock Creek follows its western edge for a mile and flows through Rock Creek Gorge cut across a part of it. The Owens River Gorge cuts through it across the whole transect.

MAJOR PLANT COMMUNITIES IN THE TRANSECT

A conspectus of the major plant communities in the transect is given in Table I, in which the important species are referred to their habitats. In the table, as well as in the following account of the map of the plant communities in the transect, an attempt has been made to name only the abundant and characteristic species rather than to give exhaustive lists. The extensive nature of this study does not permit a detailed account of more than a few species. The vegetation-types are distinct in character and appearance within the region, and there is little difficulty in recognizing the major communities as follows:

- | | |
|---|---|
| <i>a.</i> Great Valley Grassland | <i>g.</i> Alpine Communities |
| <i>b.</i> Foothill Woodland | <i>h.</i> Subalpine Forest (east slope) |
| <i>c.</i> Chaparral | <i>i.</i> Lodgepole Forest |
| <i>d.</i> Western Yellow Pine Forest | <i>j.</i> Jeffrey Pine Woodland |
| <i>e.</i> Fir-Lodgepole Forest | <i>k.</i> Sagebrush |
| <i>f.</i> Subalpine Forest (west slope) | |

Within the areas dominated by each of the major communities listed above, vegetation of other growth-forms is locally represented. It is convenient to describe the vegetation in the order of these major communities. Within the area of each, the herbaceous, shrubby, and tree communities are described. In the tabular conspectus of associations each one of these types is divided further on the basis of habit differences. It was impracticable to indicate all of these smaller units on the map, where only the larger divisions are shown together with specially noteworthy occurrences of particular dominant species represented by means of symbols.

In the following account a survey is made of the major plant communities as they would be encountered in traveling eastward within the strip. Following this description the special ecological features within the strip are pointed out. At the end, mention is made of a number of unexpected occurrences of dominant species at considerable distances from their areas of continuous distribution. Several of these occurrences extend the known range of the species involved.

Great Valley Grassland

The greater part of the Great Valley Grassland area within the transect represents an overgrazed weedy phase of the native California bunch grass association, dominated by *Stipa pulchra*³ and several other species. At the present time the native herbaceous plants within this area are obscured by the great abundance of Mediterranean weeds, chief of which are *Avena fatua*, *Erodium botrys* and *E. cicutarium*, *Hordeum* spp. and *Bromus* spp. In moist places *Cynodon dactylon* and *Holcus halepensis* are abundant. During spring and early summer many native herbs grow in great abundance over wide areas. Among the more abundant and conspicuous of these are *Brodiaea capitata*, *Layia playglossa*, *Orthocarpus purpurascens*, *Eschscholtzia californica*, *Allo-carya stipitata*, *Gilia tricolor*. Species of *Claytonia*, *Calandrinia*, *Nemophila*, *Castilleja*, *Lupinus*, *Trifolium*, *Amsinckia*, and others are present.

The hog-wallow formation is very characteristic of the eastern side of the Great Valley. It is present in the western part of the transect, especially near El Prado. The characteristic species of the formation are *Boisduvalia cleistogama*, *B. glabella* var. *campestris*, *Navarretia leucocephala*, *Downingia elegans*, *D. ornatissima*, *Mimulus tricolor*, *Lepidium latipes*, *Psilocarphus brevis-simus*, *Lythrum californicum*, *Orcuttia californica*, and around the border of the depression *Juncus bufonius* and *Lolium temulentum*.

In several depressions in the flood plain where standing water persists until summer the Tule Marsh association is present. The characteristic species are *Scripus acutus*, *S. californicus*, and *Typha latifolia*.

The tree vegetation of the Great Valley Grassland area is limited to the river banks and flood plain of the San Joaquin River. The important trees are *Salix nigra*, *S. lasiandra*, *Populus fremontii*, and *Platanus racemosa*. A few trees of valley oak, *Quercus lobata*, also occur here. Associated with these trees on the river banks are *Salix sessilifolia* var. *hindsiana*, *Rosa californica*, and *Cephalanthus occidentalis*.

Foothill Woodland

The lower "foothill" region is characterized by open stands of blue oak, *Quercus douglasii*, in which the ground cover is grassland composed of the same species as inhabit the general surface of the Great Valley. At slightly higher elevations is the lower limit of digger pine, *Pinus sabiniana*, and that

³ Except where otherwise indicated, all plant names are according to W. L. Jepson ('25).

of *Ceanothus cuneatus*, *C. integrerrimus*, and *Arctostaphylos mariposa*. Also occurring in the foothill region are *Aesculus californica*, *Quercus wislizenii*, and *Rhamnus californica*. These are especially abundant on the shoulders of Little Table Mountain and Table Mountain and on the river terrace above Friant. A xeric shrubby growth of *Lupinus albifrons*, and *Senecio douglasii*, and *Nicotiana glauca*, a tall ruderal from South America, is common on the river terrace. *Lupinus albifrons* is very abundant in places on Table Mountain where it grows to 8 feet in height.

The stream side association of this area consists of the same willow species as are found where the river flows through the Great Valley Grassland area. In addition to the willows, we find *Alnus rhombifolia*, the first tree of which was noted below Old Fort Miller at 300 feet above sea level. *Salix lasiandra* and *Platanus racemosa* are scattered along the stream bed of Little Dry Creek, the former forming a separate association in several places along a tributary of this temporary stream west of the Millerton School.

In several localities on the rocky slopes of Table Mountain and hills near it the low bushy perennial, *Lotus scoparius*, forms nearly pure stands; *Lupinus nanus* var. *vallicola* is associated with it in places.

The northward slopes of Table Mountain are heavily wooded where protection from the sun makes possible a closed growth of the above mentioned shrubs and trees. In these situations species characteristic of higher elevations are also present, such as *Umbellularia californica*, *Fraxinus dipetala*, *Cercis occidentalis*, and *Myrica hartwegii*.

Selaginella bigelozii occurs in thick mats on the walls of Table Mountain with a northward exposure and at higher elevations. *Pellaea mucronata* is frequently associated with it.

Chaparral

The Chaparral is a very distinctive vegetation made up of many shrub species most of which are evergreen. The characteristic species in the part of the transect dominated by Chaparral are *Ceanothus cuneatus*, *C. integrerrimus*, *C. divaricatus*, *Arctostaphylos mariposa* (at the lower elevations), *A. viscida*, and *Cercocarpus betuloides*. Other species occurring within the transect are *Dendromecon rigida*, *Eriodictyon californicum*, *Ericameria arborescens*, *Cercis occidentalis*, *Fremontia californica*, *Rhamnus crocea* var. *ilicifolia*, *Carpenteria californica*, *Quercus dumosa*, *Symphoricarpus mollis*, and *Holodiscus discolor*. *Quercus douglasii* and *Pinus sabiniana* occur scattered throughout the Chaparral, the former being most abundant at the lower elevations. *Quercus wislizenii* and *Q. chrysolepis* are common, the latter forming dense stands on the sides and bottoms of side canyons of Big Creek canyon. *Torreya californica* occurs rather frequently in the upper part of the Chaparral area, ranging as high as 6,000 feet. *Acer macrophyllum* and *Staphylea bolanderi* are present in the Chaparral near the lower limit of the Yellow Pine Forest into which they range for a short distance.

Within the Chaparral area are small local openings in which is found grass-land vegetation consisting of such species as *Lotus scoparius*, *Eriophyllum caespitosum*, *Gnaphalium californicum*, *Clarkia romoboides*, *C. elegans*, *Brodiaea capitata*, *B. laxa*, *Godetia viminea*, *Madia elegans*, *Castilleja breweri*, and species of *Grindelia*, *Hemizonia*, *Calandrinia*, *Lupinus*, *Mentzelia*, *Layia*, *Viola*, and others.

Western Yellow Pine Forest

The Western Yellow Pine Forest is dominated by *Pinus ponderosa* with incense cedar, *Libocedrus decurrens*, in smaller numbers. The stand is usually open. Sugar pine, *Pinus lambertiana*, is scattered through the upper part of the area, ranging higher than *P. ponderosa*. *Pseudotsuga taxifolia*, the Douglas fir, the common associate of yellow pine over so widespread a territory, has been observed in only one part of the transect. This locality, which is near the limit of its range in the Sierra, is between Power House No. 1 at Cascada and Kerckhoff Dome and southeastward in the direction of Tamarack Mountain.

The black oak, *Quercus kelloggii*, is the only important broad-leaved tree ranging throughout the Yellow Pine Forest. It has a very scattered distribution. In the lower half of the area the mountain dogwood, *Cornus nuttallii*, grows in the shaded side canyons. The white alder, *Alnus rhombifolia*, is also present in great abundance occurring in somewhat more sunny situations than the dogwood.

In the upper part of its range the Yellow Pine Forest merges into the Fir-Lodgepole Forest. This is the condition at Huntington Lake (7,000 feet) where *P. ponderosa* var. *jeffreyi* occupies the sunny exposed situations in several places forming local pure stands. In this region it is associated with aspen, *Populus tremuloides*, as at Lakeshore, Huntington Lake, Poison Meadow, in the canyon of the South Fork, and in Mono Creek canyon above Vermilion Valley. On the northward slopes south of Cascada and above The Saddle on the Cascada-Huntington Lake road *Abies magnifica* ranges downward well into the Yellow Pine Forest.

The shrubs of the Yellow Pine Forest are an important part of the vegetation of the area. Several very distinctive communities of shrubs occur, consisting of species of *Ceanothus*, *Arctostaphylos*, *Castanopsis*, *Ribes*, and *Prunus*. Species of *Aralia*, *Rhododendron*, *Symphoricarpos*, *Chrysothamnus*, *Pentstemon*, *Sambucus*, etc., also occur. At the lower limits of the area the chaparral species and forest species overlap somewhat, but the lower limits of the forest proper are distinctly defined. Starting not far from the Chaparral-Yellow Pine Forest boundary on the slopes of Bald Mountain and extending upward and eastward for a number of miles is a continuous association of mountain misery (kit-kit-dizzy), *Chamaebatia foliolosa*.

In the upper part of the forest *Ceanothus cordulatus*, *Arctostaphylos patula*, and *Castanopsis sempervirens* form extensive thickets on the more open

slopes and sharply defined thickets in open places on the forest floor. Intimately associated with them are *Ribes* sp. and *Prunus* sp.

The herbaceous vegetation of the Yellow Pine Forest presents a great variety of forms. In open dry places in the forest such herbs as *Stipa elmeri*, *Allium campanulatum*, *Asarum hartwegii*, *Gayophytum diffusum*, *Wyethia helmioides*, *Gilia aggregata*, and species of *Arabis*, *Calochortus*, *Brodiaea*, *Eriogonum*, *Streptanthus*, *Clarkia*, *Convolvulus*, *Bromus*, etc., occur. In the meadows and meadowy places along streams and on mesophytic slopes the following species are representative: *Allium validum*, *Lilium pardalinum*, *Veratrum californicum*, *Habenaria leucostachys*, *Dodecatheon jefferyi*, *Lupinus superbus*, *Geranium richardsonii*, *Guem marcrophyllum*, *Phacelia californica* and species of *Potentilla*, *Mimulus*, *Ranunculus*, *Aquilegia*, *Hypericum*, *Saxifraga*, and *Trifolium*. The meadows of the Yellow Pine Forest area are frequently bordered by dry flats in which sedge species* are usually dominant. On rock walls and in rock crevices in damp shady situations *Saxifraga aestivalis* and species of similar requirements are abundant.

Fir-Lodgepole Forest

The Fir-Lodgepole Forest is composed of a denser stand of trees than is the Yellow Pine Forest. It is dominated along its lower margin by white fir, *Abies concolor*, and at higher elevations by red fir, *Abies magnifica*, and lodgepole pine, *Pinus contorta*.⁴ The red fir occurs in several places in pure stands as indicated on the map. Lodgepole frequently does so, covering extensive areas including a great variety of habitats. *Pinus lambertiana* is scattered through this forest on the southward slopes of Kaiser Ridge north of Huntington lake. *Juniperus occidentalis* occurs on more exposed slopes and ridges, especially in the vicinity of Kaiser Pass.

The *Ceanothus*, *Arctostaphylos*, and *Castanopsis* species with their *Ribes* and *Prunus* associates which form thickets and extensive brushy areas on slopes in the upper part of the Yellow Pine Forest, form like communities in the lower part of the Fir-Lodgepole Forest area, where they are best developed on exposed slopes. In addition to this shrub association there are two others which are distinctly characteristic of this forest. The commoner of these two is the Pine-Mat Manzanita association, *Arctostaphylos nevadensis*. The plants of this species are gregarious and roughly carpet the forest floor in places north of Huntington Lake, along the trail which follows the North Fork of Mono Creek, and elsewhere. The second association is that formed by Red Heather, *Phyllodoce breweri*, in places along Big Creek above Huntington Lake and near the upper limit of *Pinus contorta* in Mono Creek Canyon.

The shrub vegetation of the forest forms a distinctive community on the talus slopes at the base of the north wall of Mono Creek Canyon east of Ver-

* *Pinus contorta* Loudon. Sudworth ('08).

million Valley. This community is indicated with a special type of shading on the map and is referred to as Talus Chaparral. The following species are important in this area: *Arctostaphylos patula*, *Ceanothus cordulatus*, *Quercus chrysolepis* (shrub height), *Quercus vaccinifolia*, *Artemisia tridentata*, *Purshia glandulosa*, *Cercocarpus ledifolius*, *Ledum glandulosum*, *Castanopsis sempervirens*, and in moister situations *Populus tremuloides*, which also forms extensive pure thickets here, and *Salix* sp.

Mountain meadows are frequent in the area of the Fir-Lodgepole Forest and meadowy places are very common along creeks on local gentle slopes. The herbaceous vegetation of these situations is similar to that of the same type of habitats as occur in the Yellow Pine Forest.

On the shaded floor of the forest such characteristic species as *Pirola secunda*, *P. picta*, *Sarcodes sanguinea*, *Corallorrhiza maculata*, *Habernaria unalaschensis*, *Pterospora andromeda*, *Pleuricospora fimbriolata*, *Lewisia leana*, etc., are found. *Pedicularis semibarbata* and *Arabis* spp. are common in less shaded situations. In larger open places where the soil consists of rather fine granite-gravel, pussy's paws, *Calyptridium unbellatum*, occurs in nearly pure associations, the plants never completely covering the surface of the ground, but the individual rosettes are usually spaced close together. At Lakeshore, Huntington Lake, it occurs with *Astragalus oxyphysus* (?), *Lupinus bicolor*, and *Gayophytum diffusum*.

In the crevices and in the granite-gravel soil of granite outcrops *Sedum obtusatum* is associated with *Potentilla santolinoides*.

Vermilion Valley is an extensive sedge flat on which *Pinus contorta* grows in dense stands near Mono Creek and in more open stands as one leaves the creek. Several species of *Carex* dominate the red tinted granite-gravel valley floor. In spring *Hesperochiron pumilus* and *Ranunculus alismaefolius* var. *hartwegii* grow in great abundance in the more open situations. In the low wet places at the lower end of the valley and Boggy Meadow, *Eleocharis bolanderi* (?) and *Scripus* sp. (?) are dominant.

Subalpine Forest (west slope)

The Subalpine Forest of the west slope is characterized by the presence of *Pinus albicaulis*, *P. monticola*, and *Tsuga mertensiana*. In this region *Pinus monticola* ranges in the upper part of the Fir-Lodgepole Forest near its upper limit and intermingles to a small extent with *Pinus albicaulis*. *Tsuga mertensiana* occurs on the rocky crest of Kaiser Ridge north and east of Huntington Lake and on the north slope of Bear Ridge, where it is sparingly present in the dense Fir-Lodgepole Forest. *Juniperus occidentalis* ranges into the area of the Subalpine Forest on Kaiser Ridge.

The characteristic shrub vegetation consists of *Salix lemmonii*, *Ledum glandulosum*, and *Kalmia polifolia* var. *microphylla*, *Ribes cereum*, *R. montigenum* in wet situations, and *Vaccinium dumosus*, *Pentstemon newberryi*,

Leptodactylon pungens in the drier situations. The granite gilia, *Leptodactylon pungens*, is abundant on granite-gravel flats and slides.

The herbaceous vegetation of the area is characterized by *Castilleia culbertsonii*, *Orthocarpus pilosus*, *Lewisia nevadensis*, *Oxyria digyna*, *Aster andersonii*, and species of *Eriogonum*, *Erigeron*, *Pedicularis*, *Epilobium*, *Lupinus*, et cetera.

Alpine Communities

The Alpine Communities are situated above timber line. No trees occur here, and the shrub vegetation is very much reduced. The meadows are dominated by *Carex breweri*, *Trisetum congdoni*, *Orthocarpus pilosa* var. *monensis*, *Solidago decumbens*, *Gentiana simplex*, and species of *Saxifraga*, *Potentilla*, *Trifolium*, *Castilleia*, *Epilobium*, and others. On the granite-gravel slopes and in the shelter of rocks *Arabis platysperma*, *Draba Lemmoni*, *Achillea borealis*, *Potentilla breweri*, *P. gordonii*, *Lupinus lyallii*, *Aquilegia pubescens* are found.

Subalpine Forest (east slope)

Pinus albicaulis is the only tree in the Subalpine Forest of the east slope. The shrubs and herbaceous vegetation associated with it are similar to those of the corresponding area on the west slope.

Lodgepole Forest

Pinus contorta dominates the Lodgepole Forest. It forms nearly pure stands over its entire range. In places *Juniperus occidentalis* is associated with it, and, where it grows on mesophytic slopes and around meadows, aspen occurs with it. The herbaceous vegetation is similar to that of the Fir-Lodgepole Forest of the Huntington Lake region in the Lodgepole Forest area. The stream and lake borders are dominated by willow and aspen.

Artemisia tridentata and *Cercocarpus ledifolius* dominate extensive areas in the Lodgepole Forest area, ranging upward from the Sagebrush growing on open exposed slopes in the upper part of their range and to within a few feet of Rock Creek in places lower down.

Jeffrey Pine Woodland

The Jeffrey Pine Woodland is dominated by *Pinus ponderosa* var. *jeffreyi*. On the eastern front of the Sierra in this region the tree occurs in open irregular stands with *Juniperus occidentalis*. Along the banks of Rock Creek it is associated with *Salix* sp. and *Betula fontinalis*.

Sagebrush

Artemisia tridentata dominates the Sagebrush, ranging over the whole eastern front of the Sierra and eastward over Volcanic Tableland. The important associates of this plant are: *Purshia tridentata*, *P. glandulosa*, and

Chrysothamnus nauseosus. On Volcanic Tableland *Chamaebatiaria millefolium*, *Ceanothus greggii*, *Chamaebatia foliolosa* are also frequently present, and *Leptodactylon nuttallii* is very abundant. *Cercocarpus ledifolius*, *Pinus monophylla*, and *Juniperus occidentalis*, *Amelanchier alnifolia*, *Prunus andersonii* occur with it on desert slopes. On Volcanic Tableland *Pinus ponderosa* var. *jeffreyi* is abundant, forming an open woodland.

NOTABLE ECOLOGICAL CONDITIONS WITHIN THE TRANSECT

The outstanding ecological feature within the transect is the eastward extension of the plant communities dominant at lower elevations to considerably higher elevations on the north wall (south aspect) of the San Joaquin River Canyon, and its eastward extension within the strip along Big Creek Canyon. This condition is also very evident in Mono Creek Canyon, which parallels the transect. It is noted on a smaller scale in the canyon of Big Creek above Huntington Lake, in the canyon of Rancheria Creek which flows into Huntington Lake from the east, and in Bear Creek Canyon, which is one of the two main canyons opening into the canyon of the South Fork.

A comparison of the limits of the different plant communities within the transect makes the basis for this generalization more apparent. In the case of the Chaparral and the Western Yellow Pine Forest communities the difference in the upper limit of the one and the lower limit of the other on opposite sides of the canyon is very impressive. The upper limit of the Chaparral and the lower limit of the Western Yellow Pine Forest is near the 4,000 foot contour on the south wall (north aspect) of the San Joaquin River Canyon (Bald Mountain). On the north wall the corresponding limits are near the 5,500 foot contour above Big Creek. In Mono Creek Canyon and Bear Creek Canyon a similar comparison could be made.

The second important ecological feature is a corollary of the first. It is that in every case of the larger communities within the transect, the lowest altitudinal range of a community is on a north-facing slope, usually a north-east exposure; and its highest range is on a south-facing slope, usually a southwest exposure.

The effect of insolation in modifying the geographical range of a vegetation-type is very noticeable in Rock Creek Canyon. The canyon is in a nearly north-south position, and the sun therefore directly illuminates its entire area when it is at its highest point. The sun's rays strike the eastern wall of the canyon during a greater part of the day. The result is seen in the distribution of the vegetation. *Artemisia tridentata*, *Cercocarpus ledifolius* and other desert species attain a much higher altitude than usual (to 10,100 feet) on the east wall of the canyon.

Rock Creek Canyon terminates in a number of large cirques at the base of Mt. Mills (13,352), Mt. Abbott (13,736), Mt. Dade (13,635), Bear Creek Spine (13,705), and two unnamed peaks (12,887 and 12,750). These cirques

contain small remnants of glaciers, and the whole upper part of the canyon has a distinctly alpine climate. The effect upon the vegetation is very noticeable, since there is an abrupt change from the alpine type of vegetation to the desert type in a short distance.

EXTRATERRITORIAL DISTRIBUTION OF CERTAIN PLANTS

The occurrence of *Artemisia tridentata*, *Purshia glandulosa*, and *Cercocarpus ledifolius*, all of which are Great Basin plants, on the west slope of the Sierra in upper Mono Creek Canyon is a striking instance of species occurring at a distance from their normal area. In this locality they are associated with the species of the Talus Chaparral on well-insolated slopes.

Pinyon, *Pinus monophylla*, was observed in a restricted locality near the west end of Bear Ridge overlooking the South Fork of the San Joaquin River. A hundred or more trees occur here on an exposed southwest slope associated with *Pinus ponderosa*, *Juniperus occidentalis*, *Arctostaphylos patula*, *Quercus vaccinifolia*, and other plants of the upper Western Yellow Pine Forest.

Two instance of plants far out of their usual range seem worthy of mention. The first of these is the observation of a single incense cedar, *Libocedrus decurrens*, on the south bank of the San Joaquin River in the foothill region at an elevation of 300 feet. The tree was about 8 inches in diameter. The second instance is that of a few trees of *Pinus monticola* growing in the upper part of the gorge of the Owens River. The elevation here is 7,000 feet.

The total absence from our part of the Sierra of *Adenostoma fasciculatum*, the narrow-leaved evergreen rosaceous shrub which is so characteristic of dry chaparral nearly throughout its range, is noteworthy. According to Cooper ('22) it is unknown in the southern part of what we consider the middle Sierra, and none has been found by the writer.

SUMMARY

By using photostat enlargements of U. S. Geological Survey topographic maps as a base map, the major plant communities in a representative belt transect 7 x 80 miles of the middle Sierra Nevada Mountains of California were determined and mapped during 1926-1930, preliminary to more detailed quantitative study of the ecological problems within the transect. From west to east the major communities are Great Valley Grassland, Foothill Woodland, Chaparral, Western Yellow Pine Forest, Fir-Lodgepole Forest, Subalpine Forest (west slope), Alpine Communities, Subalpine Forest (east slope), Lodgepole Forest, Jeffrey Pine Woodland, and Sagebrush. In a conspectus of these major communities the herbaceous, shrubby, and tree communities are distinguished on the basis of habitat differences. Only the larger divisions are shown on the map, with specially noteworthy occurrences of particular dominant species indicated by means of symbols. The outstanding ecological feature within the transect is the eastward extension of

the plant communities dominant at lower elevations to considerably higher elevations on the north wall of the San Joaquin River canyon and other canyons which parallel the transect in a general west to east position. The occurrence of *Artemisia tridentata*, *Purshia glandulosa*, and *Cercocarpus ledifolius*, Great Basin species, on the west slope at some distance from their normal area, and the total absence of *Adenostema fasciculatum*, characteristic of dry chaparral nearly throughout its range, are noteworthy.

The writer desires to express his appreciation and thanks to Dr. A. G. Vestal, University of Illinois, under whose supervision most of the work was done at Stanford University, and because of whose continued interest and encouragement this project has been brought to its present form, and to Mrs. Roxana S. Ferris, of the Dudley Herbarium, Stanford University, for assistance rendered in the determination of many species and for reading the manuscript.

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PHYSIOGRAPHIC AND FAUNAL AREAS IN THE ATHABASKA AND GREAT SLAVE LAKES REGION

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In the summer of 1914 a party from the Geological Survey of Canada made a traverse from Lake Athabaska to Great Slave Lake by way of the Tazin and Taltson Rivers. Nearly all of this route lay through previously unexplored territory, and numerous geographical features of the region were then mapped for the first time. The expedition was in charge of Mr. Charles Camsell, of the Geological Survey staff, whose report ('16) deals mainly with the geological and geographical results.

The present paper forms a small portion of my own report as the zoologist of the party. In its preparation use has been made of a few additional records that were obtained on a trip to Lake Athabaska in 1920, under the auspices of the United States Biological Survey. A hitherto unrecognized faunal area lying east of Slave River, between Lake Athabaska and Great Slave Lake, is described and named herein, and some of the adjacent physiographic and faunal areas are also discussed.

Physiographic Areas

In view of the important relation existing between physiographic areas and faunal areas, it will be well to consider briefly the physiography of the southern portion of the Mackenzie Basin. Our knowledge of this subject has been well summarized by Camsell and Malcolm ('19, pp. 9-40; Fig. 1, p. 10), from whose paper much of the following information under this section is quoted.

The Mackenzie Basin south of Great Slave Lake and east of the Rockies is occupied by two major physiographic divisions, the Great Central Plain and the Laurentian Plateau. The boundary between these two divisions "is a fairly well-defined line marked by the contact between the Pre-Cambrian crystalline or metamorphic rocks [on the east] and the flat-lying Palaeozoic sedimentary rocks [on the west]. This line of contact enters the Mackenzie Basin from the south at Methye portage on Clearwater River in longitude 110 degrees west. Running northwesterly from there it passes the east [= west] end of Athabaska Lake and follows the valley of Slave River to Great Slave Lake" (p. 11).

THE GREAT CENTRAL PLAIN

The Great Central Plain is composed of two main subdivisions, the Alberta Plateau and the Mackenzie Lowlands. The former has a northeasterly

slope and "covers virtually the whole region south and southwest of Great Slave Lake" (p. 17). The latter "commences in the lower part of Peace River and the extreme western end of Lake Athabaska, whence it extends as a narrow band down the valley of Slave River to Great Slave Lake. . . . It embraces the basin of the western end of Great Slave Lake and continues thence down the valley of Mackenzie River to the Arctic Coast" (pp. 19-20). The northern boundary of the Alberta Plateau "is marked by a series of north facing escarpments which extend from near Fort Smith on Slave River northwesterly along the south side of Great Slave Lake and thence at an equal distance along Mackenzie River to the Liard in longitude 122 degrees" (pp. 17-18). From a general level of about 2,500 feet above the sea toward the south end of the Mackenzie Basin, the Great Central Plain slopes gradually northward or northeastward to a level of about 700 feet at Lake Athabaska and about 520 feet at Great Slave Lake. The general surface "is monotonous and outcrops of the solid rocks are rare, and because the drainage is immature, muskegs are abundant and lakes fairly numerous" (p. 18). The Great Central Plain as a whole is thickly wooded, though there are many areas of open prairie land, especially along the middle course of the Peace River.

THE LAURENTIAN PLATEAU

That portion of the Laurentian Plateau extending from Great Slave Lake south to the Churchill Basin seems to fall into two main subdivisions, though the region has been so imperfectly explored that this classification may be regarded as only provisional. Lake Athabaska forms the approximate boundary between the two subdivisions. South of this lake "is a large area underlain by horizontally bedded sandstone which on decomposition forms wide plains of sand or gently rounded hills and ridges wooded with banksian pine" (p. 14). Tyrrell (1896, p. 10d) found the country along Cree and Black Rivers predominantly sandy, comparatively level, and moderately wooded, the underlying rocks for the most part being covered with sand. Probably similar conditions will eventually be found over most of the area between Lake Athabaska on the north, Wollaston Lake on the east, the Churchill Basin on the south, and the Athabaska Valley on the west.

North of Lake Athabaska the physiographic conditions are strikingly different from those on the south. They have been described at some length by Camsell ('16, pp. 10-19), from whose paper the following excerpts are taken.

"It is a country, when viewed on a large scale, of moderate relief and rounded outline, but in detail it is rugged, broken, and rocky. It abounds in lakes, and its streams flow in ill-defined and irregular valleys, rarely more than 100 feet deep.

"The highest elevations in the region are on the immediate shores of Athabaska Lake where the hills rise somewhat abruptly to a maximum height of about 700 feet above the lake or about 1,400 feet above the sea. From there, the surface slopes gradually and regularly, northwest, to Great Slave Lake. . . .

"Over the greater part of the region the bed-rock has no covering of soil nor loose material. Here and there sand-plains or patches of boulder clay occur; and, towards the mouth of the [Taltson] river, the bed-rock is covered by sediments from Slave River. . . .

"All the solid rocks of the region are of Pre-Cambrian age. . . .

"Over the surface of the solid rocks are spread thin and scattered deposits of Glacial and post-Glacial drift material. . . .

"One of the most marked features of the region is the evidence of the intensity of the glaciation with the resulting freshness and unweathered character of the rock surface. . . . In general, the region is characterized by glacial erosion and removal of material rather than by glacial deposition."

Many details of the physiography of this region are presented in Camsell's report ('16, pp. 44-77).

Faunal Areas

RELATION TO PHYSIOGRAPHIC AREAS

With this review of the physiographic areas of the Mackenzie Basin south of Great Slave Lake, we may proceed to a consideration of the faunal areas. While there is a certain relation between the two, there is not an exact correspondence. The former have been differentiated largely on the basis of the underlying rocks. But where these rocks are mostly covered with soil, adjoining portions of the two major physiographic divisions may not exhibit very striking or important differences of soil, climate, vegetation, or fauna. This seems to be actually the case with the Laurentian region south of Lake Athabaska and the Alberta Plateau on its western border. Therefore they may be included, at least for the present, in the same faunal area.

Furthermore, the upper portion of the Slave River valley and the lower portion of the Taltson River valley, below the mouth of Tethul River, are both included in the Laurentian Plateau on the basis of the underlying pre-Cambrian rocks. In both of these areas, however, the rocks have been largely covered up with alluvial soil, with the result that the faunal affinities of these areas are distinctly with the Great Central Plain on the west instead of with the Laurentian Plateau on the east. If the physiographic areas were based upon surface conditions, such as soil, rather than upon the underlying rocks, there would evidently be a much closer correspondence in some cases between the physiographic and the faunal areas.

On the other hand, a single physiographic area undoubtedly includes adjoining parts of both the Canadian and the Hudsonian Zones in the Laurentian Plateau between Lake Athabaska and Great Slave Lake. In this particular case two faunal areas are differentiated chiefly or wholly by the factor of temperature; but this factor does not suffice to bring about a corresponding differentiation of physiographic areas. (Cf. Distributional Factors, below.)

Whatever faunal differences there may be between adjoining portions of the Alberta Plateau and the Mackenzie Lowlands, from the Liard River to the western end of Lake Athabaska, they appear so slight and gradual that they may be disregarded, at least until further explorations result in the ac-

cumulation of many more distributional data. The increase in latitude in this region is partly compensated for by the decrease in altitude; and this condition also obtains in the Laurentian Plateau on the east of the Slave River.

THE TAZIN HIGHLANDS

Boundaries

If, in the light of our present (and still very imperfect) knowledge of the distribution of animal and plant life in the region immediately south of Great Slave Lake, one were to divide that region into life zones as conceived by Merriam (1894), then the boundary between the Canadian and the Hudsonian Zones might be traced somewhat as follows. Beginning on Great Slave Lake a short but indefinite distance east of the mouth of the Taltson River, it would pass southeastward to Soulier and Hill Island Lakes and probably to the eastern end of Tazin Lake. Continuing in the same direction, it would reach the north shore of Lake Athabaska in the vicinity of Beaver River, about 65 miles from the eastern end of the lake. Thence it would pass close to Black and Wollaston Lakes and reach Reindeer Lake at about its middle. It must be borne in mind, however, that the boundary between two life zones as slightly differentiated as the Canadian and the Hudsonian¹ can hardly be represented adequately by a single line; a broad band, with somewhat indefinite borders, would serve better as an indication of actual conditions.

Throughout the greater part of the Canadian Zone south of Great Slave Lake the faunal conditions seem to be moderately uniform. Of course the limits of distribution of certain species are reached here and there at different points, but for the most part there are no very abrupt or striking changes. An exception, however, is found in a portion of the Canadian Zone lying north of Lake Athabaska and east of the Slave River. This seems to constitute a distinct faunal area,² for which the name of "Tazin Highlands" (Fig. 1) is here proposed.

This area may be considered roughly triangular in shape. Though its boundaries have been explored only here and there, they may be tentatively defined as follows. On the northeast, from Great Slave Lake to Lake Athabaska, it is bounded by the Hudsonian Zone (see above). The entire southern and western boundaries may be fixed approximately wherever the greater portion of the land surface on the one side is composed of exposed rocks,

¹ These two zones have been treated from a botanical standpoint by Macoun and Malte ('17, p. 4) as a single unit under the name of 'Subarctic Forest Zone.'

² Cf. Dice ('22, p. 335): "A *biotic area*, then, may be defined as a geographic district, characterized by an assemblage of species and of ecological characteristics differing from those found in adjacent areas. A biotic area will usually, though not always, be also a climatic area, and will often be a distinct physiographic area as well." The manner in which the Tazin Highlands answer to this definition of a biotic area will be shown in the following pages.

and on the other, of alluvial or other soil. On the south the approximate boundary is Lake Athabaska, though certain low-lying portions of the western half of the north shore belong faunally (and to some extent geologically) with the sandy region south of this lake. The exposed rocks of the Tazin

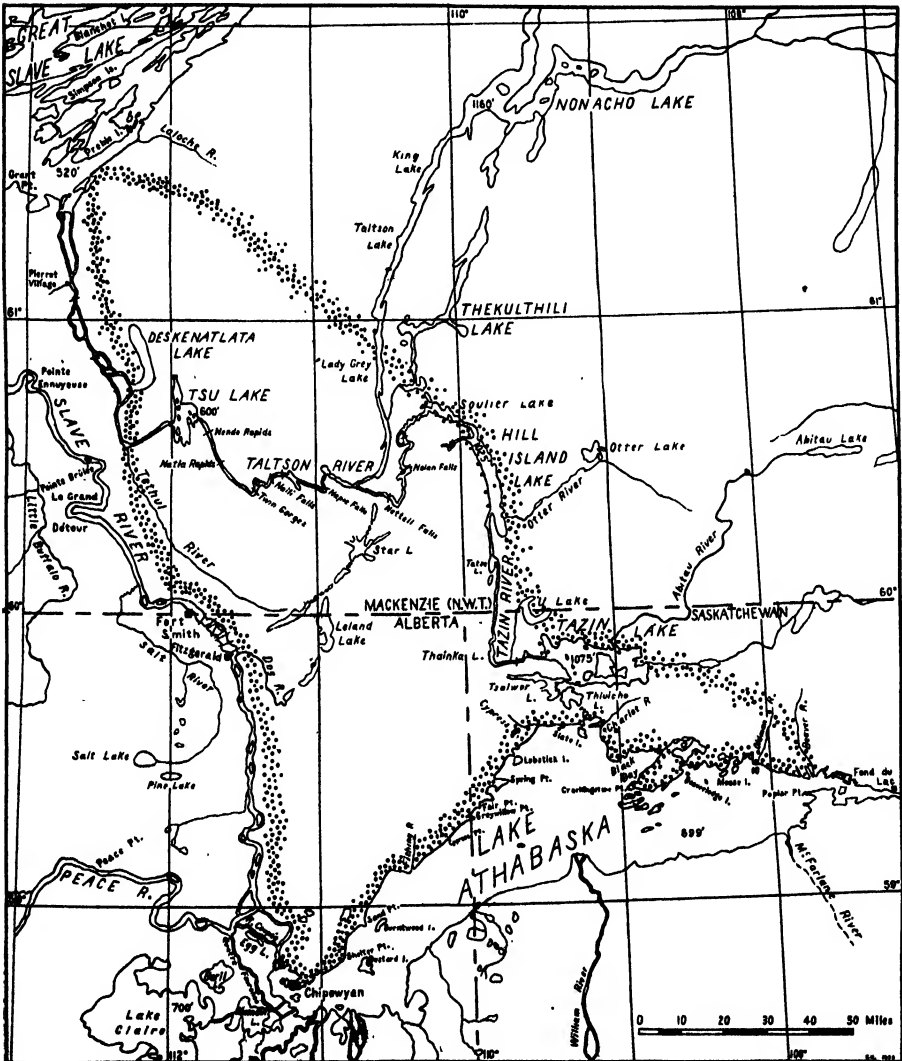


FIG. 1. Region between Lake Athabaska and Great Slave Lake. Approximate boundary of the Tazin Highlands faunal area indicated by a dotted band.

Highlands extend directly to the lake, however, in many places quite to its western end, and there are bold outcrops of the same rocks rising here and there in the Quatre Fourches marshes and in the adjoining delta of Peace River. The western boundary probably parallels the Slave River, at a very

short distance east of this stream, from the vicinity of Chipewyan to the junction of the Taltson and Tethul Rivers. From this point to Great Slave Lake the boundary extends probably almost due north, on the east side of the Taltson, through an area that has not yet been explored.

At the junction of the Taltson and Tethul Rivers an abrupt change in topography, vegetation, and fauna furnishes a striking illustration of the differences between the Tazin Highlands and the adjoining part of the Canadian Zone. To the eastward the terrain is composed mostly of rugged hills



FIG. 2. Summit of a hill on the eastern side of Tsu Lake, Mackenzie, with sparse and stunted jack pines (*Pinus Banksiana*) growing on lichen-covered rocks. Tazin Highlands faunal area. August 9, 1914. (Reproduced by courtesy of the Geological Survey of Canada.)

of exposed bed-rock, sparsely clothed with stunted timber (Fig. 2). To the westward the land is comparatively low and flat, and except for a few scattered outcrops of granite or gneiss the surface is composed of soil. The timber is comparatively dense and tall, forming a continuous forest (Fig. 3). In the more open parts a thick growth of grasses and other herbs marks a conspicuous change from conditions to the eastward. Such birds as the king-bird, white-throated sparrow, and red-eyed vireo, which had not been observed in the Tazin Highlands, were found here.

Distributional Factors

The topography, soil, rocks, humidity, and rainfall seem to be essentially the same on both sides of the ill-defined boundary between the Tazin Highlands and the adjoining portion of the Hudsonian Zone.³ Likewise, there can be no very appreciable difference in altitude, although the general southwesterly trend of the chief watercourses on the northeastern side of the



FIG. 3. Comparatively well-forested area along the Taltson River in the latitude of Deskenatlata Lake, Mackenzie. Trees mostly aspen poplar (*Populus tremuloides*). Canadian Zone, just outside of the Tazin Highlands faunal area. August 12, 1914. (Reproduced by courtesy of the Geological Survey of Canada.)

boundary indicates a slightly greater elevation in the Hudsonian Zone. To all appearances, therefore, temperature is in this case not only the controlling but practically the sole factor bringing about that gradual differentiation of vegetation and fauna which marks the transition from one zone to another. The boundary evidently coincides closely with an isothermal line.

³ In discussing the nature of boundary lines between physiographic areas, Fenneman ('17, p. 25) remarks: "It may thus happen that the major divisions are locally separated by very poorly defined lines while nearby lines separating minor divisions may be very bold." The same remark applies very aptly to such a faunal area as the Tazin Highlands, its northeastern boundary (where it adjoins the Hudsonian Zone) being poorly defined, while its southern and western boundaries (where it adjoins other portions of the Canadian Zone) are rather sharply defined.

On the other hand, it is quite evident that among the various factors which affect distribution, there are others besides temperature which distinguish the Tazin Highlands from adjoining parts of the Canadian Zone (e.g., the Slave River valley).

The chief and fundamental distinguishing factor is a physiographic (or geological) one—the scantiness or absence of soil. This in turn results in sparseness of vegetation, and thereby has an important effect on the distribution of animal life.

There is probably a slight lowering of temperature in the Tazin Highlands,

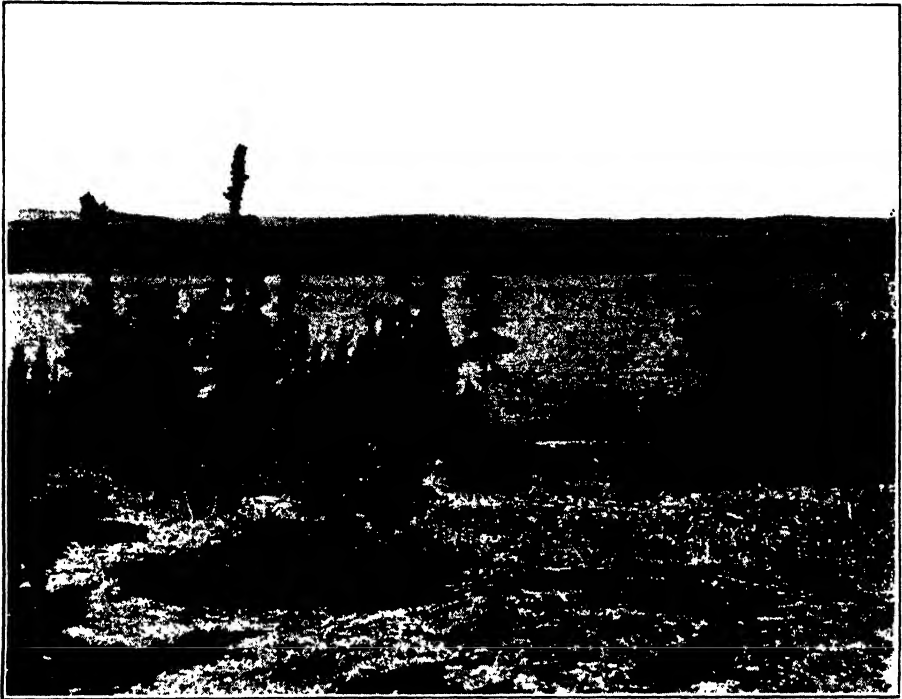


FIG. 4. An island and the north shore of Lake Athabaska between Moose Island and Oldman River, Saskatchewan. Black spruce (*Picea mariana*) and canoe birch (*Betula papyrifera*) in the foreground. Tazin Highlands faunal area, approaching conditions of the Hudsonian Zone. August 13, 1920. (Reproduced by courtesy of the U. S. Biological Survey.)

on account of the slightly increased altitude and the greater proximity of the Barren Grounds. The difference in temperature is not alone sufficient, however, to account for the various faunal changes.

Probably there are no pronounced differences in rainfall or winds. The average annual precipitation at Chipewyan for a period of 10 years is only 20.21 inches, and in the summer of 1914 we found the rainfall very light. The prevailing winds over this area during the same season seemed to be southerly and westerly.

Humidity is perhaps a little less in the Tazin Highlands, where bare rocks, scanty soil, and steep slopes permit rapid drainage, and where evaporation, because of the comparative sparseness of the vegetation, probably does not take place in such large quantity as in the adjacent and more heavily forested lowlands. If it is true not only that humidity increases vegetation, but that increase in vegetation tends to produce greater humidity—then, with the same

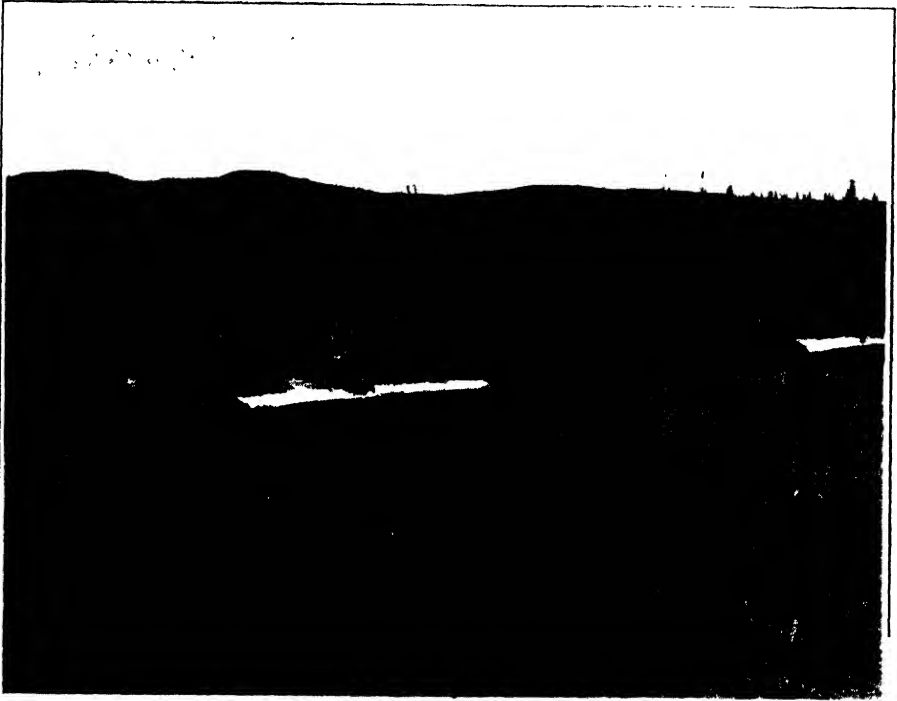


FIG. 5. North shore of Lake Athabaska from Slate Island, Saskatchewan. Trees largely spruce. Tazin Highlands faunal area. August 19, 1920. (Reproduced by courtesy of the U. S. Biological Survey.)

amount of precipitation, the Tazin Highlands would be likely to have slightly less humidity than the Slave River valley.

Vegetation

The removal of most of the former covering of soil by intense glaciation has had a marked effect upon the vegetation. The timber is more or less sparse and stunted, particularly on the rocky sides and summits of the hills (Figs. 2, 4, 5). Everywhere, however, lichens clothe the rock exposures, and the scantiest amount of loose material suffices to furnish the jack pine with a foothold. Along the valleys and in the muskegs the better conditions of soil and moisture enable the trees to attain a somewhat larger size and denser growth.

The trees and more important shrubs of the Tazin Highlands, listed somewhat in the order of their abundance, are the following :

Trees

<i>Pinus Banksiana</i>	Jack pine
<i>Picea canadensis</i>	White spruce
<i>Picea mariana</i>	Black spruce
<i>Betula papyrifera</i>	Canoe birch
<i>Populus tremuloides</i>	Aspen poplar
<i>Larix laricina</i>	Tamarack
<i>Populus balsamifera</i>	Balsam poplar

Small Trees or Large Shrubs

<i>Salix</i> spp.	Willows
<i>Alnus</i> spp.	Alders
<i>Betula</i> (<i>glandulosa</i> ?)	Dwarf birch

Shrubs

<i>Arctostaphylos Uva-ursi</i>	Bearberry
<i>Ledum groenlandicum</i>	Labrador tea
<i>Vaccinium Vitis-Idaea</i> var. <i>minus</i>	Mountain cranberry
<i>Cornus canadensis</i>	Bunchberry
<i>Rosa acicularis</i>	Wild rose
<i>Viburnum pauciflorum</i>	Few-flowered viburnum
<i>Amelanchier alnifolia</i>	Northwestern serviceberry
<i>Myrica Gale</i>	Sweet gale
<i>Vaccinium uliginosum</i>	Bog bilberry
<i>Vaccinium canadense</i>	Canada blueberry
<i>Rubus melanolasius</i>	Red raspberry
<i>Juniperus communis</i> var. <i>depressa</i>	Juniper
<i>Ribes oxycanthoides</i>	Northern gooseberry
<i>Shepherdia canadensis</i>	Canadian buffalo-berry
<i>Prunus pennsylvanica</i>	Wild red cherry
<i>Ribes prostratum</i>	Skunk currant
<i>Empetrum nigrum</i>	Crowberry
<i>Andromeda Polifolia</i>	Wild rosemary

Practically all of the above-mentioned species are likewise common in the adjoining parts of the Canadian Zone. Both the aspen poplar and the balsam poplar (particularly the latter) are limited to a much smaller size here than in the Slave River valley. The other trees also, as well as some of the shrubs (such as *Amelanchier* and *Prunus*), are similarly affected to a greater or less extent. Smaller size and sparser growth, therefore, seem to constitute the chief differences between the vegetation (at least as far as the trees and shrubs are concerned) of the Tazin Highlands and that of adjoining parts of the Canadian Zone.

Unfortunately a considerable part of the country appears to have been swept time and again, and with disastrous effect, by forest fires, some of which are set purposely by the Indians in order to temporarily improve the hunting.

Fauna

A comparison of the fauna of the Tazin Highlands with that of adjacent areas brings out some interesting differences and resemblances.⁴

The first of the following lists comprises species whose northward distribution, outside of the Tazin Highlands, is limited approximately by the boundary between the Canadian and the Hudsonian Zones. The ranges of some extend slightly beyond the boundary, while the ranges of others fall a little short. All alike, however, are typical of the Canadian Zone, except in the Tazin Highlands. From the greater part of this area, so far as known at present, they are practically or totally absent, though some must be expected to be found within its western and southwestern borders, where the altitude of the plateau averages considerably less, and where climatic conditions are tempered also by the influence of neighboring valleys and lowlands.

Canadian Zone Species Absent from the Tazin Highlands

Mammals

<i>Mephitis hudsonica</i>	Northern Plains skunk
<i>Marmota monax canadensis</i>	Canadian woodchuck
<i>Eutamias minimus borealis</i>	Liard River chipmunk
<i>Bison bison athabasca</i>	Wood buffalo

Birds ⁵

<i>Bonasa umbellus umbelloides</i>	Gray ruffed grouse
<i>Sphyrapicus varius varius</i>	Yellow-bellied sapsucker
<i>Phloeotomus pileatus abieticola</i>	Northern pileated woodpecker
<i>Tyrannus tyrannus</i>	Eastern kingbird
<i>Empidonax minimus</i>	Least flycatcher
<i>Molothrus ater artemisiae</i>	Nevada cowbird
<i>Agelaius phoeniceus fortis</i>	Thick-billed redwing
<i>Quiscalus quiscula aeneus</i>	Bronzed grackle
<i>Zonotrichia albicollis</i>	White-throated sparrow
<i>Spizella pallida</i>	Clay-colored sparrow
<i>Piranga ludoviciana</i>	Louisiana tanager
<i>Bombycilla cedrorum</i>	Cedar waxwing

⁴ It must be borne in mind, however, that the incompleteness of our data renders some of the following statements and conclusions more or less tentative.

⁵ Although the ranges of water birds, with their specialized habitats, do not usually conform to life zones so clearly as do those of land birds, the following species might perhaps be added to the present list: *Chlidonias nigra surinamensis*, *Pelecanus erythrorhynchos*, *Querquedula discors*, *Marila collaris*, *Botaurus lentiginosus*, *Porsana carolina*, *Fulica americana*, and *Oxyechus vociferus vociferus*.

<i>Vireosylva olivacea</i>	Red-eyed vireo
<i>Vireosylva gilva swainsoni</i>	Western warbling vireo
<i>Lanivireo solitarius solitarius</i>	Blue-headed vireo
<i>Mniotilta varia</i>	Black and white warbler
<i>Dendroica tigrina</i>	Cape May warbler
<i>Dendroica magnolia</i>	Magnolia warbler
<i>Dendroica palmarum palmarum</i>	Palm warbler
<i>Seiurus aurocapillus</i>	Ovenbird
<i>Setophaga ruticilla</i>	Redstart

The absence of many of these species from the Tazin Highlands may well be accounted for by their preference for a more heavily forested country. In some cases, therefore, sparseness of vegetation may be a more effective barrier to northward distribution than low temperature.

The next list is like the foregoing in so far as it comprises species whose northward distribution is practically limited by the boundary between the Canadian and the Hudsonian Zones. Unlike those in the preceding list, however, the following species are found in the Tazin Highlands nearly or quite to the border of the Hudsonian Zone. In comparison with the species in the first list, these would seem to be affected rather more by temperature, and rather less by vegetation, as distributional factors.

Canadian Zone Species Present in the Tazin Highlands

Mammals

<i>Eutamias amoenus</i>	Athabaska red-backed mouse
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Birds

<i>Mergus americanus</i>	American merganser
<i>Nuttallornis borealis</i>	Olive-sided flycatcher
<i>Myiochanes richardsoni richardsoni</i>	Western wood pewee
<i>Empidonax flaviventris</i>	Yellow-bellied flycatcher
<i>Melospiza melodia juddi</i>	Dakota song sparrow
<i>Sitta canadensis</i>	Red-breasted nuthatch
<i>Hylocichla guttata pallasi</i>	Eastern hermit thrush

Amphibians

<i>Rana pipiens</i>	Leopard frog
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The following species differ from those in the last preceding list in having slightly more northerly limits to their ranges. While typical of the Canadian Zone, they have also been recorded in the Mackenzie Basin at various points within the Hudsonian Zone, such as Rae or Good Hope. They have been found more or less throughout the Tazin Highlands as far as the border of the Hudsonian Zone.

Species Ranging through the Tazin Highlands and into the Hudsonian Zone

Birds

<i>Picoides arcticus</i>	Arctic three-toed woodpecker
<i>Sayornis phoebe</i>	Eastern phoebe
<i>Spizella passerina arizonae</i>	Western chipping sparrow
<i>Melospiza georgiana</i>	Swamp sparrow
<i>Vermivora celata celata</i>	Orange-crowned warbler
<i>Vermivora peregrina</i>	Tennessee warbler
<i>Hylocichla ustulata swainsoni</i>	Olive-backed thrush

Certain species, such as *Ceryle alcyon alcyon* and *Riparia riparia riparia*, are distributed through both the Canadian and the Hudsonian Zones, yet seem to be practically or totally absent from the Tazin Highlands. In the present cases this may be readily accounted for by the lack of suitable banks of sand or clay for nesting-sites.

The following typically Hudsonian species have been found at the breeding season along the northeastern border of the Tazin Highlands:

Birds

<i>Archibuteo lagopus sancti-johannis</i>	American rough-legged hawk
<i>Pinicola enucleator alascensis</i>	Alaska pine grosbeak
<i>Zonotrichia leucophrys gambeli</i>	Gambel's sparrow
<i>Spizella monticola monticola</i>	Eastern tree sparrow
<i>Hylocichla aliciae aliciae</i>	Gray-cheeked thrush

Zonotrichia leucophrys gambeli also breeds at many points in the upper Canadian Zone from Resolution westward, and has even been found sporadically during the summer at Fitzgerald and Chipewyan. The last two species in the above list, however, evidently do not breed south of the Hudsonian Zone; and in the territory between Athabaska and Great Slave Lakes the southern limit of their breeding ranges is about as satisfactory a criterion as has yet been discovered for marking the southern border of this zone. The Surf Scoter (*Oidemia perspicillata*) seems to breed mainly in the Hudsonian Zone, but has also been found during the summer at various places in the Tazin Highlands.

Until recent years, at least, the Barren Ground Caribou (*Rangifer arcticus arcticus*) in its winter migrations spread over much of the Tazin Highlands, but passed south of this area to only a limited extent, and west of it probably not at all. There seems to be a significant correlation between its distribution at this season and the occurrence of exposures of pre-Cambrian rocks, on which its favorite food (*Cladonia*) grows in especial abundance.

From the foregoing comparisons it will be seen that the faunal differences between the Tazin Highlands and adjacent parts of the Canadian Zone are probably more numerous than those between the Tazin Highlands and ad-

jacent parts of the Hudsonian Zone. In view, however, of the practical absence of Hudsonian forms from this area and of the presence of certain forms that are not Hudsonian, it seems necessary to consider it a part of the Canadian Zone.

Summary

There is not an exact correspondence between physiographic and faunal areas in the Mackenzie Basin south of Great Slave Lake. The former have been differentiated largely on the basis of the underlying rocks, while the latter are determined by such factors as soil, climate, and vegetation.

The boundary between the Canadian and Hudsonian Zones in this region is placed approximately along a line extending from Great Slave Lake, at a point a little east of the mouth of the Taltson River, southeastward past Hill Island Lake to Lake Athabaska at the mouth of Beaver River. (The further extension of the boundary in this direction leads to Reindeer Lake at about its middle.) The area bounded by this line, the lower Taltson River valley, the upper Slave River valley, and Lake Athabaska, represents a distinct faunal area, for which the name of "Tazin Highlands" is proposed. It lies wholly within the Laurentian Plateau.

Temperature is practically the sole factor bringing about a gradual differentiation of vegetation and fauna between the Tazin Highlands and the adjoining portion of the Hudsonian Zone. From the adjoining parts of the Canadian Zone the Tazin Highlands are differentiated by scantiness of soil (resulting from intense glaciation), sparseness of vegetation, a slight increase in altitude, and perhaps slightly lower temperature and less humidity.

The trees and shrubs of the Tazin Highlands are Canadian Zone species, but they are generally limited here to a smaller size. Among the land vertebrates considered typical of adjoining parts of the Canadian Zone, 1 mammal, 7 birds, and 1 frog are listed as likewise typical of this faunal area, while 4 mammals and 21 birds are listed as practically or totally absent from it. Five typically Hudsonian birds were met with along the northeastern border of the Tazin Highlands. The southern limit of the breeding ranges of *Spizella monticola monticola* and *Hylocichla aliciae aliciae* is the most satisfactory criterion found for marking the boundary between the Hudsonian and Canadian Zones.

Since the Tazin Highlands lack only a part of the typical Canadian species, but practically all of the typical Hudsonian species, this area is considered a part of the Canadian Zone.

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INFLUENCE OF TEMPERATURE AND MOISTURE UPON THE NATURE AND EXTENT OF DECOMPOSITION OF PLANT RESIDUES BY MICROORGANISMS

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Introduction

Climate markedly modifies the nature and rapidity of decomposition of plant remains in the soil and thus exerts an important influence upon the nature and abundance of the organic matter, or so-called "humus." It is an entirely wrong assumption that this "humus," simply because it is dark in color and is found in the soil, always comprises the same constituents, in terms of definite chemical complexes. The chemical nature of the "humus" will depend upon: (1) the chemical nature of the plant residues; (2) the soil conditions, such as reaction, aeration, abundance of available minerals, etc., all of which modify the nature of the microscopic population of the soil which bring about the decomposition processes; (3) the environmental or climatic conditions, especially temperature and moisture supply, which modify not only the nature of the microorganisms but also the rate of the decomposition processes; (4) finally the type of microorganisms active in the decomposition of the plant residues, as influenced by the above factors.

The problems commonly considered in the study of decomposition of plant residues, as influenced by climatic conditions, comprise: (1) the decomposition of the organic residues as a whole, as well as of the various chemical constituents; (2) the accumulation of "humus" which is more resistant to further decomposition than the fresh plant residues; (3) the rate of evolution of the plant nutrients in an available form.

According to Mohr ('22), no organic matter accumulates in well aerated soils at an average temperature of 25° C. and higher. When the mean temperature is below 25° C., organic matter accumulates even in fully aerated soils. The lower the temperature the greater will be the accumulation of organic matter in the soil, within certain limits. This he explained by the relative influence of the temperature upon the growth of higher plants and upon the development of microorganisms which destroy the plant residues. The lower temperatures check the growth of the latter more than of the former. As a result, organic matter, in the form of plant residues, will be produced quicker than it can be destroyed by microorganisms. In water-logged soils, the aerobic fungi and bacteria are unable to develop, due to the prevailing anaerobic conditions, while certain higher plants grow readily.

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The anaerobic organisms capable of living under these conditions are unable to decompose the plant residues as fast as they accumulate. Therefore, peat will be formed even in regions of prevailing high temperatures. These ideas were later substantiated by Sensi (1925).

Jenny (1928a) found that a correlation exists between the mean annual temperature and the nitrogen content of the soil. The logarithm of the nitrogen was shown to vary inversely with the temperature. For every decline of 10° C. in the mean annual temperature, the average nitrogen content increases 2 to 3 times. The carbon-nitrogen ratio of the soil organic matter was also found (Jenny, 1928b) to be materially influenced by the temperature, the ratio becoming wider with decreasing temperature. The large organic matter content in soils at high altitude (Alpine soils) was shown to be due to the delayed action of microorganisms because of the low annual temperature (Jenny, 1926).

According to Hesselman (1926) and Lang (1926), the higher organic matter content in the forest soils of northern regions as compared with southern regions is due to the influence of climate on the growth of the higher vegetation, on the one hand, and the organic matter decomposing microorganisms, on the other.

The following investigations were undertaken with the purpose of throwing light upon these phenomena under controlled laboratory conditions. The experiments deal with the factor of influence of temperature and moisture upon the decomposition processes of plant residues as a whole, and of the various constituents in particular, as well as with the nature of the microorganisms active in these processes. In the study of the decomposition of organic matter by microorganisms, methods have been developed (Waksman and Stevens, 1928, 1930) which may enable one to follow not only the course of decomposition of the plant residues as a whole, but also that of their various chemical constituents.

Experimental

MATERIALS AND METHODS

Oat straw has been selected as a source of plant material to be subjected to decomposition by a mixed microbial flora and fauna.

One hundred and thirty gram quantities of air-dry straw, equivalent to about 120 gm. of oven-dry material, were placed in a series of glazed porcelain pots. Some of the pots received no additional mineral nutrients, while others received each 5 gm. $(\text{NH}_4)_2\text{HPO}_4$, 1 gm. KCl, 0.5 gm. $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$, and 5 gm. CaCO_3 . One half of the composts containing the added inorganic nutrients received 200 per cent water (on the basis of the dry material) and the other half 400 per cent,² giving two series of composts which contained 66.6 per cent and 80 per cent moisture on the basis of total weight. The composts without the additional nutrient salts were prepared with the lower moisture content only, namely 66.6 per cent. All of the pots were covered

² This was equivalent to 240 and 480 cc. of water respectively for the 120 gm. of material.

with plates and incubated at 4 different temperatures: (1) at 6-8° C., in an electric refrigerator (average 7° C.); (2) at room temperature, ranging from 15° to 21° C., with an average of 18° C.; (3) in an incubator kept at 25-28° C. (average 27° C.); (4) in an incubator kept at 35 to 40° C. (average 37° C.). All composts were inoculated with the same suspension of soil.

At different intervals of time the composts were well mixed and aliquot samples removed for analysis. The moisture content was then again brought up to 66.6 and 80 per cent according to the original plan. Some of the analyses were made directly on the fresh moist material; for some analyses, the samples of the composted material had to be first dried to remove the excess of water. The results were calculated on the basis of the total compost left in each pot at the time of sampling, so as to be comparable with the original material used. At all subsequent samplings, account has been taken of the amounts previously removed, and results again calculated on the basis of the total material originally introduced into the pots.

The results are always recorded both on a relative, percentage basis of the residual material and upon a total quantity basis, as compared with the quantity of the original plant material used in preparing the composts. Table I

TABLE I. *Chemical composition of fresh oat straw*
Relative and total concentration of chemical constituents, on dry basis

Chemical constituent	Composition of straw without addition of nutrient salts, per cent	Composition of straw with addition of nutrient salts, per cent	Total amount of chemical complexes, gm.
Total straw used.....	100	100	120.25*
Ether-soluble fraction.....	1.93	1.75	2.30
Cold water soluble organic matter....	8.05	7.34	9.66
Hot water soluble organic matter....	3.46	3.16	4.15
Alcohol-soluble fraction.....	1.76	1.60	2.11
Hemicelluloses.....	19.50	17.80	23.40
Cellulose.....	34.91	31.84	41.89
Lignin.....	12.98	11.82	15.58
Total nitrogen.....	0.492		0.592†
Ash.....	5.55	10.49	6.66†

*Without the added salts; with added salts 11.5 gm. more.

†Nitrogen and ash content of the original straw.

gives the chemical composition of the fresh oat straw. Although only about 120 gm. of the original dry material was used, in the form of straw, one should recall that 11.5 gram portions of different inorganic salts were also added to some of the composts. As a result of this, the ash and nitrogen content in the pots receiving the inorganic nutrients became considerably higher than in the original straw.

RATE OF DECOMPOSITION

The first analysis was made after 16 days' incubation of the various composts. The material kept at the lowest temperature was not analyzed at that

time due to the fact that there was no visible decomposition. The same is true of the composts receiving no additional inorganic salts. In making the analyses the residual material in each compost was carefully weighed and the moisture content determined; aliquot portions were then removed for the analyses. The results are calculated on the basis of the total residual dry material. Table II gives the percentage of the original amount of material left at different times and temperatures.

TABLE II. *Amount of compost left, after decomposition for various periods of time, at different temperatures*

On per cent basis of total original material

Temperature of incubation, ° C.	Moisture content, per cent	Days of incubation			
		16	48	105	* 273
7*.....	66	—	—	99.4	76.4
7.....	66	—	—	73.7	64.3
7.....	80	—	—	77.8	63.7
18.....	66	—	63.3	53.2	49.5
18.....	80	81.7	60.2	46.7	39.2
27*.....	66	—	72.0	56.0	36.4
27.....	66	66.7	51.2	44.1	35.3
27.....	80	67.5	46.4	37.6	29.9
37*.....	66	—	72.1	51.8	40.1
37.....	66	64.2	48.6	39.8	30.0
37.....	80	61.0	39.4	32.0	23.6

* Composts without nutrient salts.

The outer appearance of the contents of the pots, after 16 days' decomposition, differed considerably in accordance with temperature and nutrients added. The material at 37° and with the 80 per cent moisture content was black-brown on the top and yellow at the bottom, where some water had accumulated. The whole mass was overgrown with fungi to such an extent that it seemed as if within 2 weeks at least 50 per cent of the plant material had been replaced by a mass of fungus mycelium. Microscopic examination showed the fungi to penetrate all the material; the celluloses were readily disintegrated, as shown by the ease with which the straw could be broken up. The compost with 60 per cent moisture looked and smelled like stable manure; it was also overgrown with fungi, though microscopically great numbers of bacteria could also be seen. At 27°, the decomposition was much less intense, the color was lighter; at 18° and 7° decomposition was only beginning. In the absence of added nutrient salts decomposition was much delayed, the growth of the fungi and bacteria being far less abundant than with nutrients.

The second series of samples was taken after 48 days' incubation. At that time the composts containing no added nutrient salts were also analyzed; the composts kept in the refrigerator at 7° still showed very little visible decomposition. At 27° and 37°, the outer appearance of the material was already much more like real "humus." At all temperatures above 7°, there

was a notable decrease in volume. The composts kept at 18° looked brown, while those at 27° were much more decomposed and gave the impression of brown "loose peat." The contents of the pots at 37° and 66.6 per cent moisture had a dark brown to black color, whereas those with the higher water content consisted largely of a brown slimy mass of material, which was found to consist mostly of bacterial cells and disintegration products.

Within the period of 48 days, there has disappeared, on the average, 38.3 per cent of the total original material at 18°, 57.4 per cent at 27° (as compared with 28.0 per cent, in the absence of added nutrients, at the same temperature) and 56.0 per cent at 37° (as compared with 27.9 per cent, in the absence of added nutrients). Here again, the higher the temperature of incubation of the compost, the greater was the amount of decomposition that has taken place. After a period of 48 days' decomposition, there was left, at 37°, 44 per cent of the original material. If we consider the fact that 23.5 per cent of this material is made up of the gradually accumulating mineral constituents, the degree of decomposition will be found to be even greater. There was no very marked difference in the composts kept at different moistures, the higher saturation giving somewhat greater decomposition.

In the absence of inorganic nutrients the decomposition was comparatively limited, even at 18° and 27°, in spite of the fact that the original oat straw had a fairly large amount of nitrogen. The material without nutrients at 37° was fairly well decomposed.

The third sampling was made after 105 days' incubation of the composts. At this time all the composts were analyzed. There was still comparatively little decomposition in the case of the composts incubated at 7°. In the absence of the inorganic nutrients there was practically no decomposition at all, while only about 24 per cent of the material disappeared in the composts that received the inorganic salts.

As to the composts containing the added nutrients and incubated at the various higher temperatures, decomposition proceeded now only very slowly. The composts without the nutrients decomposed now more rapidly, due to the fact that they were still rich in cellulose and hemicelluloses.

After 105 days, the composts with nutrients kept at 7° began to show a somewhat darker color than those without nutrients; though the latter had a white mycelium throughout the mass of straw, decomposition had not yet set in to a notable degree.

The fact that the composts incubated at 37° were reduced from 44 per cent of the original, after 48 days of incubation, to 36 per cent of the original, after 105 days of incubation, indicates that these composts have already been reduced to a certain resistant state and that further decomposition will take place only very slowly; the readily decomposable constituents, including the cellulose and hemicelluloses, have disappeared rapidly during the earlier period of 48 days. The carbohydrates were reduced to a minimum so that their slow decomposition does not influence markedly the changes in the bulk

of the compost. The lignins have now been undergoing only very gradual decomposition, while the organic nitrogenous complexes continued to accumulate.

The last complete analysis was carried out after the composts had been incubated for 273 days. Some of the composts, namely, those kept at 27° and 37°, in the presence of added inorganic salts, were reduced to a condition which would be termed in common parlance "completely humified." The material, especially with the higher moisture content, was largely colloidal in nature and could pass for pure "humus." When both moisture contents were averaged, they represented only 26.8 per cent of the original material, in

TABLE III. *Influence of temperature upon the transformation of nitrogen in the decomposition of oat straw*

Period of incubation days	Temperature ° C.	No inorganic nitrogen added		Inorganic nitrogen* and other minerals added	
		Total nitrogen gm.	Proteins* gm.	Total nitrogen gm.	Proteins* gm.
0.....	—	0.590	2.472	—†	2.472
16.....	18	—	—	—	3.715
16.....	27	—	—	1.478	6.350
16.....	37	—	—	1.462	6.455
48.....	18	—	—	1.344	6.580
48.....	27	0.508	1.930	1.286	6.580
48.....	37	0.655	2.920	1.292	6.530
105.....	7	0.660	2.110	1.630	8.005
105.....	18	—	—	1.490	7.660
105.....	27	0.642	1.810	1.217	6.715
105.....	37	0.600	2.950	1.416	7.100
273.....	7	0.633	3.260	1.473	7.733
273.....	18	—	—	1.198	6.813
273.....	27	0.594	3.044	1.024	5.920
273.....	37	0.590	3.006	1.148	6.171

* Total water-insoluble nitrogen $\times 6.25$.

† This total nitrogen comprised the nitrogen in the straw and that added in the form of five grams of ammonium phosphate.

the case of the 37° composts, and 32.6 per cent of the original in the case of the 27° composts, with an ash content of 33.0 and 28.6 per cent, respectively, of the total residual material. This residual "humus" was nearly free from cellulose, or contained only a small amount of this group of carbohydrates; it also had only a small concentration of hemicelluloses, but it was rich in lignins and modified lignins and in nitrogenous organic compounds (calculated as protein). The last two groups of compounds and the ash were found to make up nearly 75 per cent of the total residual material. A detailed study of the chemical nature of this "humus" is reserved for a later publication.

The composts kept at 18° and the two composts without the additional

nutrients kept at 27° and 37° had also undergone rapid decomposition, to a less extent, however, than the composts with the added nitrogen at the higher temperatures. The low temperature composts were still lagging considerably behind. As a matter of fact, the composts with nutrients kept at 7° decomposed in 273 days to about the same extent as the corresponding composts kept at 27° and at 37° within 16 days. Corresponding differences were obtained in the composts without inorganic salts.

The results of the nitrogen transformation are summarized in Table III. The rapid decomposition of the organic matter in the composts kept at the higher temperatures accounts for the more rapid synthesis of organic nitrogenous compounds at those temperatures. However, after prolonged incubation these compounds undergo rapid decomposition, with the result that the nitrogen is gradually liberated in an inorganic form or lost into the atmosphere. The lower temperatures of decomposition thus favor a greater preservation and accumulation of the nitrogen than the higher temperatures.

These results add further weight to the calculations made by Jenny that the total nitrogen content is lower in the soils of warmer climates and that the ratio of carbon to nitrogen is somewhat wider in soils of cooler climates. The first relation is explained by the greater accumulation and preservation of the nitrogen in the soils at lower temperatures, while the second phenomenon is due to the slower decomposition of the total organic matter, especially of the lignins (high in carbon) in the soils of cooler regions.

TABLE IV. *Influence of temperature upon the carbon-nitrogen ratio of oat straw composts decomposing at different temperatures for 300 days*

Temperature of incubation	Moisture content of compost	No inorganic nitrogen added to compost	Inorganic nitrogen added
	per cent	C/N	C/N
7° C.	66.6	90.0	22.5
	80.0	—	36.6
18° C.	66.6	—	14.7
	80.0	—	18.4
27° C.	66.6	36.9	16.4
	80.0	—	15.7
37° C.	66.6	39.3	11.8
	80.0	—	10.8

This is clearly brought out in Table IV where the data on the carbon-nitrogen ratio of the composts kept at the different temperatures are recorded. At the highest temperature, the carbon-nitrogen ratio of the material has been reduced from nearly 100 in the original straw to 11.3, or to almost the ratio found between carbon and nitrogen in normal soils. With a decrease in the temperature of incubation, this ratio widens. In other words where decomposition has been most favorable and most rapid, leading to a practically complete decomposition of the cellulose, the carbon-nitrogen ratio has become practically the same as that in the soil "humus." Here again further evidence

is brought to show that the various conceptions prevalent in the literature concerning the "humified" and "non-humified" parts of the soil organic matter are practically meaningless.

At the lower temperatures, the composts with the higher moisture have shown a wider carbon-nitrogen ratio; however, at the two higher temperatures the reverse was true. This may possibly be due to the fact that the fungi, which were more active at the lower temperatures, are unfavorably affected by the higher moisture, while the bacteria, more active at the higher temperatures, were not appreciably affected by an increase in the moisture content of the compost.

In analyzing the results of the experiments, it must be kept in mind that the compost material has been changed under the influence of a number of different factors, 4 of which have been kept more or less under control, namely, temperature, available nutrients, moisture content and period of decomposition. Since all the samples were inoculated with equal quantities of the same soil suspension, one would expect that the different microorganisms, which came into action and brought about the decomposition of the plant material, resulted from the conditions just referred to. Some of the analyses have been summarized in a number of graphs: Figures 1 and 2 show the percentage of the different constituents left after 273 days of decomposition, while figures 5-10 show the percentage of the various chemical complexes that have been decomposed at the various stages of the experiment. In these curves the gradient of the curves towards the abscissae is a measure of the rate of decomposition, whereas the angle between two different curves representing two different temperatures is a measure of the influence of temperature on the process. In those cases where material has been synthesized rather than decomposed, the curves run below the abscissa as shown in figures 9 and 10.

RELATIVE CHEMICAL COMPOSITION OF THE COMPOST MATERIAL

In analyzing the data on the relative chemical composition of the residual material in the composts at the various temperatures and after the different intervals of time, one must bear in mind the fact that the percentage of a certain substance may rise, although the actual quantity left has diminished, because other constituents have been decomposed at a more rapid rate (Table V).

Since the actual amount of ash has remained unchanged throughout the whole process (except in the composts receiving the minerals where some CO_2 was lost due to the interaction of the CaCO_3 with the organic acids produced in the decomposition), the relative composition of the ash (Fig. 2) is found to increase constantly; this may serve as an indirect measure of the rate of decomposition of the plant material as a whole. The highest percentage of ash, namely 34.8 per cent (24.4 per cent more than in the original material), is found in the compost kept at 37° and with 80 per cent moisture,

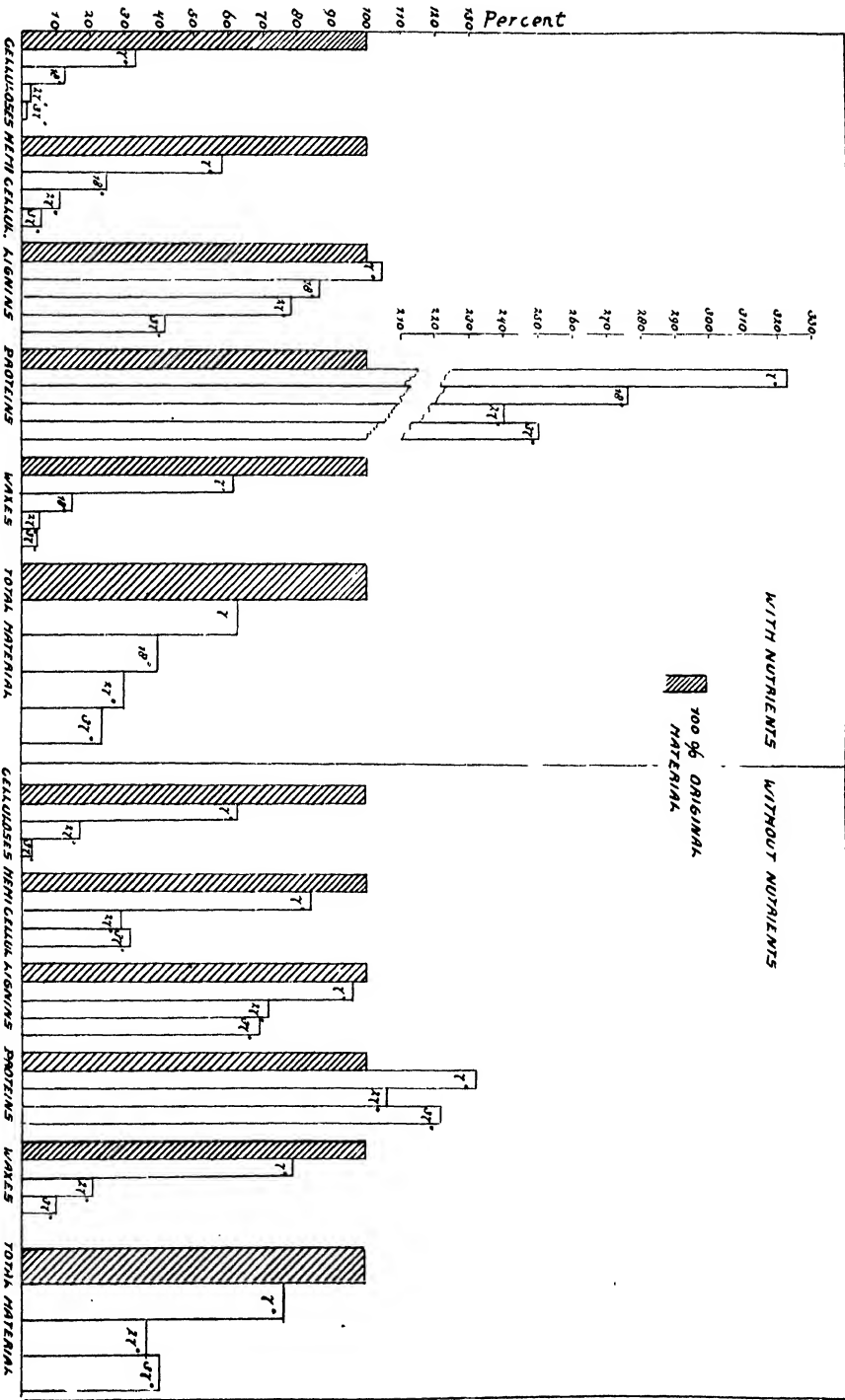


Fig. 1. Transformation of oat straw as a whole, and of its important chemical complexes at different temperatures, with and without the addition of nutrient salts, within 273 days. Results calculated on the basis of 100 gm. of original material.

TABLE V. *Relative composition of composts, after decomposing at different temperatures for various lengths of time*
 In per cent of total residual material. Figures in parenthesis refer to the concentration of the specific complex in the original straw

Tem- pera- ture of incu- bation	Mois- ture	Ether-soluble substances (1.9)		Water- soluble substances (11.6)		Alcohol- soluble substances (1.8)		Hemicelluloses (19.5)		Cellulose (34.9)		Lipens (13.0)		Proteins (2.1)		Ash (5.6 10.5)	
		Days of incubation		Days of incubation		Days of incubation		Days of incubation		Days of incubation		Days of incubation		Days of incubation		Days of incubation	
		16	48	105	273	16	48	105	273	16	48	105	273	16	48	105	273
7° C.*	66.6	—	—	1.6	2.0	—	—	—	21.6	21.4	—	—	14.1	16.9	—	5.6	7.0
7° C.	66.6	—	—	—	8.7	—	—	—	20.8	26.8	—	—	17.3	18.9	—	—	—
7° C.	80.0	—	—	1.6	1.7	—	2.7	—	16.1	16.2	—	—	14.4	19.5	—	—	—
18° C.	66.6	2.1	2.5	1.1	0.7	11.4	8.9	7.6	14.2	10.0	0.0	24.4	13.2	10.9	5.6	15.6	18.5
18° C.	80.0	2.1	2.3	0.9	0.7	9.0	9.6	7.9	15.4	10.1	11.1	26.0	13.0	10.0	10.2	10.6	19.6
27° C.*	66.6	—	1.7	1.2	1.1	—	13.8	8.7	—	20.6	18.8	15.3	18.3	10.9	9.2	9.3	18.3
27° C.	66.6	2.4	—	0.8	0.7	9.0	9.2	6.0	6.6	19.4	9.9	6.2	2.9	17.9	21.8	25.9	31.0
37° C.	80.0	2.0	0.7	0.5	0.5	9.1	10.1	7.5	13.4	9.6	20.4	26.2	22.7	—	16.0	18.4	22.3
37° C.*	66.6	0.9	0.6	0.7	0.5	—	1.2	1.4	—	20.1	18.5	15.1	4.9	23.2	14.1	9.3	7.4
37° C.	66.6	—	—	—	—	1.8	1.5	2.2	14.7	12.5	7.3	4.9	23.2	14.1	9.3	7.4	18.6
27° C.	80.0	1.1	1.4	0.3	0.3	12.2	12.4	9.5	8.3	6.7	4.3	20.9	5.4	5.3	2.3	10.8	22.9

* Composts without nutrient salts.

after 273 days of decomposition. The smallest percentage of ash, as was to be expected, is found in the compost kept at 7° without the nutrients (7 per cent after 273 days against 5.6 per cent at the beginning of the experiment).

The relative protein content of the compost shows an increase of nearly 8 times after 105 days at 37°, as compared with the original concentration of the organic nitrogenous constituents. Twenty-four weeks later, in all the experiments, only a very small relative increase is observed, notwithstanding

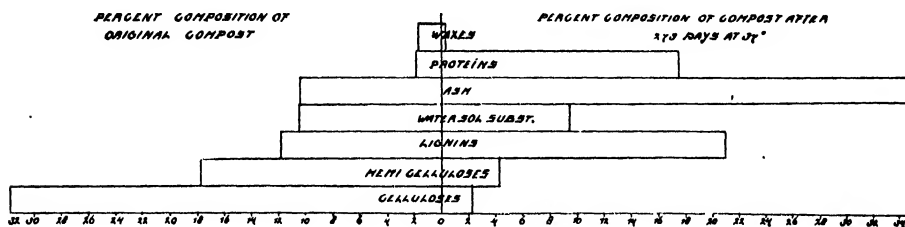


FIG. 2. Relative composition of initial plant material and of residual "humus," after 273 days of decomposition at 37° C.

the fact that the total actual concentration has already diminished, due to the reduction in concentration of the other components.

The percentage of lignins has nearly doubled after the first 105 days in almost all the pots, whereas the relative composition of the final product after 273 days shows only a small increase. The lignins are thus found to form the most abundant organic constituent of the compost decomposed at 37° (Fig. 2).

The cellulose and hemicelluloses have been greatly reduced, in some cases even to one-fourteenth of the original amount. The relative percentage of the hemicelluloses in the final product is higher than that of the cellulose, which is the reverse relation between these two polysaccharides in the original plant material. Only at the low temperature and without the added nutrients have the changes not been very radical.

The alcohol and water soluble substances have shown little change from the original concentrations, while the ether soluble substances almost disappeared with the progress of decomposition, especially at the higher temperature.

Figure 3 gives a visual representation of the change in bulk of the composts kept at the different temperatures.

NUMBERS OF BACTERIA, FUNGI AND ACTINOMYCES PRESENT IN THE VARIOUS COMPOSTS, AFTER 14 WEEKS

In order to obtain some idea of the nature of the microorganisms which were taking an active part in the decomposition of the straw in the composts at the various temperatures, dilutions were prepared by the usual procedure and 1 cc. portions plated out on albumin agar (alkaline for bacteria and ac-

tinomyces, acid for fungi). Table VI shows the relative number of the colonies from the various composts found per gram of material (averages of 3 to 4 counts).

The abundance of actinomyces in the composts at the advanced stage of decomposition shows that they must play an important rôle in the processes of decomposition of the material; they were practically absent in the composts at 27° where no nutrient salts were added. Whether this was because

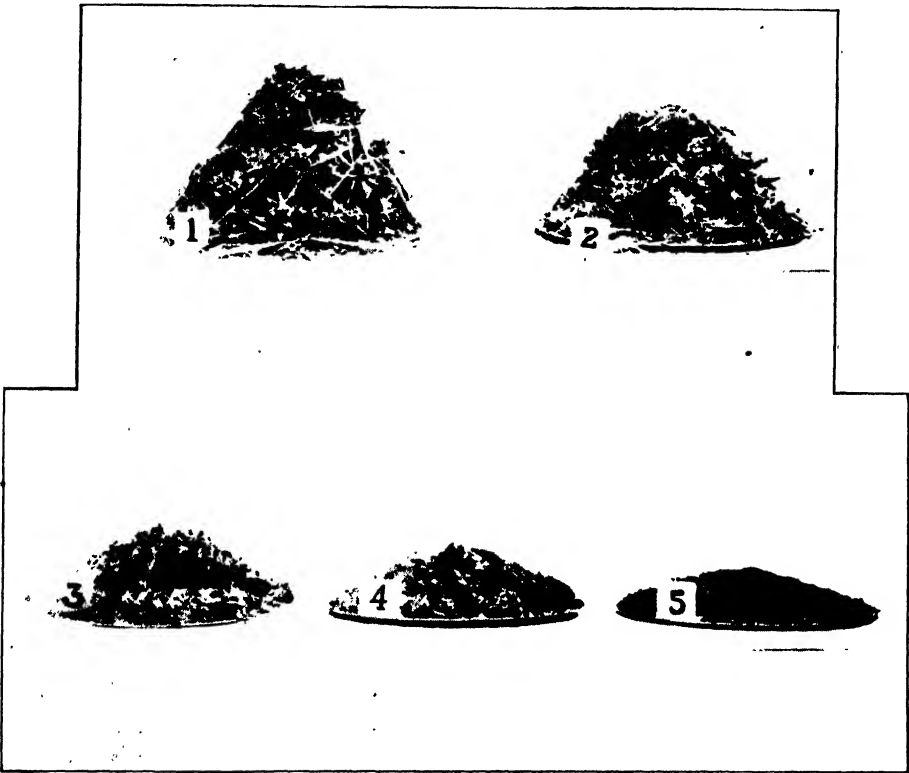


FIG. 3. Appearance of composts decomposing at various temperatures for 102 days: (1) no nutrients, at 7° C. (99.4 per cent of original weight); (2) nutrient salts added, at 7° C. (73.7 per cent of original weight); (3) nutrient salts added, at 18° C. (53.2 per cent of original weight); (4) nutrient salts added, at 27° C. (44.1 per cent of original weight); (5) nutrient salts added, at 37° C. (39.8 per cent of original weight).

TABLE VI. *Numbers of microorganisms in straw composts, after 14 weeks decomposition*

Temperature of incubation	Nutrient salts	Bacteria	Actinomyces	Fungi
27° C.....	+	95,000,000	145,000,000	50,000,000
27° C.....	-	1,118,000,000	0	10,000,000
37° C.....	+	137,000,000	243,000,000	44,000,000
37° C.....	-	108,000,000	47,000,000	30,000,000

the decomposition in this compost has not progressed as far as in those receiving nutrient salts or to some other factor remains to be determined. In half of the composts the number of actinomyces even surpassed that of the bacteria, and it seems quite necessary to pay more attention to the biochemical activities of these organisms.

The fungi, though present in smaller numbers, no doubt take a most active part in the decomposition of the organic substances; the influence of the absence of nutrient salts is shown in a reduction in the number of the fungi, which, however, is not nearly so pronounced as in the case of the actinomyces. A microscopic examination of the decomposing material showed that in course of time there was a succession of microorganisms, usually at first an abundant mycelium covering every piece of straw, afterwards bacteria taking the place of the fungi, whereas towards the end great numbers of actinomyces appeared.

CARBON DIOXIDE PRODUCTION

In order to learn more about the influence of temperature upon the activities of microorganisms, especially during the early stages of the process of decomposition, the evolution of carbon dioxide was measured for a period of 3 weeks.

One hundred gram portions of quartz sand were placed in a number of 250 cc. flasks. Two gram portions of air dry oat straw and 20 cc. of a nutrient solution containing 5 gm. $(\text{NH}_4)_2\text{HPO}_4$, 1 gm. KCl and 0.5 gm. MgSO_4 in one liter, were added to each flask. Some flasks received 0.5 gm. portions of CaCO_3 in addition to the nutrients, and others received only 20 cc. of distilled water without nutrients or CaCO_3 .

The preparations in the flasks were then inoculated with a suspension of the composts in the larger experiment. The CO_2 evolution was measured by aerating each flask one hour a day and absorbing the CO_2 in a $\text{Ba}(\text{OH})_2$

TABLE VII. *Evolution of CO_2 in the decomposition of 2 gm. of oat straw, at different temperatures*

Temperature of incubation	Treatment	Milligrams of CO_2 given off in days						Nitrogen used up per cent
		2	5	8	11	15	21	
7° C.	NS*	1.36	10.32	25.20	31.40	—	51.94	37.6
	NS + CaCO_3	4.16	12.66	27.86	34.14	—	58.80	34.6
	None	0.98	5.64	17.64	22.94	—	40.56	0
18° C.	NS	21.30	36.28	—	111.60	158.80	198.26	83.9
	NS + CaCO_3	21.50	36.38	—	118.14	172.86	233.98	87.7
	None	19.12	29.72	—	55.72	—	76.32	0
27° C.	NS	50.06	124.78	182.80	—	289.88	334.32	76.8
	NS + CaCO_3	49.66	107.56	174.20	—	312.32	366.40	85.8
	None	32.86	44.98	58.74	—	89.84	123.66	0
37° C.	NS	52.80	101.12	181.46	—	270.62	332.50	64.3
	NS + CaCO_3	45.50	102.82	187.78	—	333.94	435.46	91.0
	None	39.80	66.72	90.06	98.72	116.12	137.64	0

* NS = Nutrient salts added.

solution, then titrating back with oxalic acid. The results of this experiment are summarized in Table VII and in figure 4.

The influence of temperature is most marked at the beginning of the process, when the divergence of the curves is at a maximum. After 4 to 5 days, the curves for the composts without nutrients show a tendency to run parallel at all temperatures, which indicates that in all those cases the rate of decom-

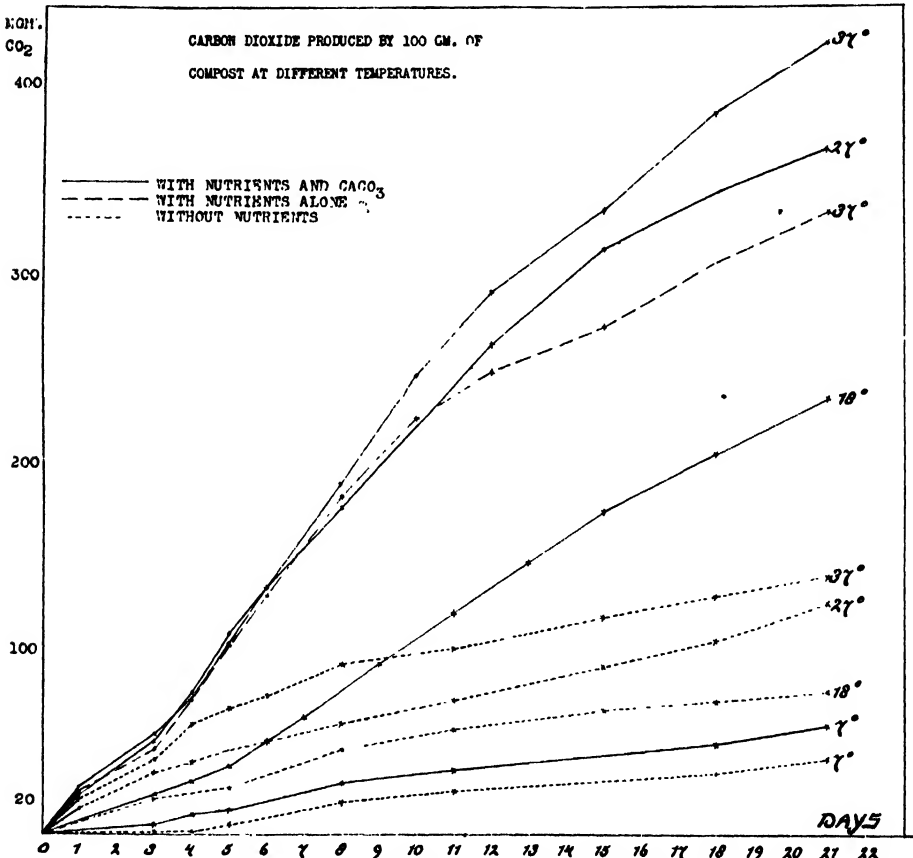


FIG. 4. Rapidity of decomposition of oat straw at different temperatures, as shown by the evolution of carbon dioxide.

position had become the same, all limited by the same factor, namely lack of available nitrogen.

An increase in temperature from 7° to 18° and from 18° to 27° resulted in a sharp increase in CO_2 production in both cases. However, the difference between 27° and 37° is much smaller, the curves nearly coinciding during the first 10 days; it seems as if the optimum temperature for decomposition has been approximately reached at 27°. When we compare the inclination of the different curves (with nutrients) to the horizontal axis, between the 15th

and the 21st day incubation periods, we see that they run approximately parallel; this means that here as well equal quantities of CO_2 are produced per unit of time in spite of the marked differences in temperature.

This is clearly brought out in figure 5, which shows that the rate of decomposition of organic matter per unit of time at all temperatures is nearly the same, after the first 16 days of decomposition. The marked differences

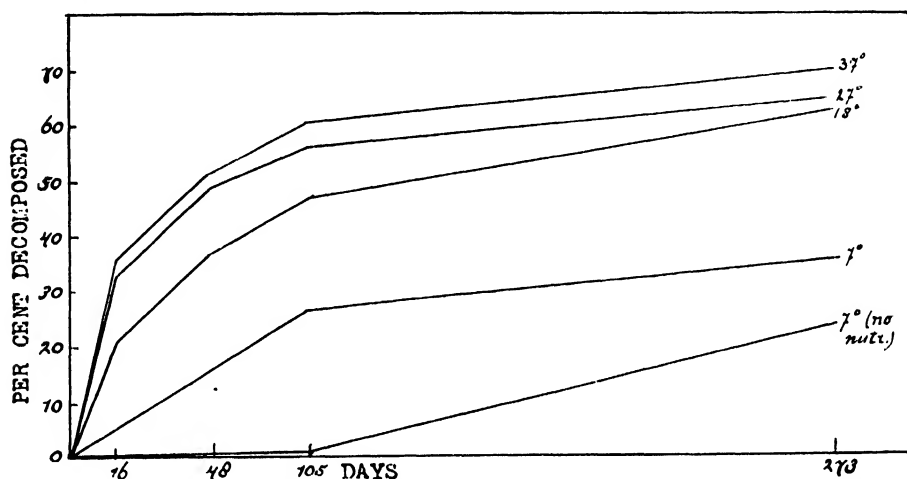


FIG. 5. Influence of temperature upon the decomposition of oat straw as a whole.

originate at the very beginning of the decomposition, namely, during the first 2 weeks.

The quantities of CO_2 produced between the 16th and the 105th days at 7°, 18°, 27° and 37° are 400, 520, 460 and 480 mgm., respectively, with an average of 466 mgm. in 89 days, for 2 gm. of dry material. The CO_2 evolution during the last period of 168 days amounts to 188 mgm. at 37° and 178 mgm. at 7°, or 1.12 and 1.06 mgm. CO_2 per day, respectively. All these data bring out surprisingly the one important fact, namely, that *within wide limits the rate of decomposition of organic matter is independent of temperature within a few weeks after the beginning of the process.*

The effect of adding nutrient salts is quite pronounced in all cases. This is demonstrated by comparing 2 corresponding curves of composts kept at one temperature with and without nutrients. The addition of CaCO_3 resulted in all cases in an increased CO_2 production, especially at 37° C. where 25-30 per cent more CO_2 has been liberated in the presence than in the absence of CaCO_3 . This points to the possibility that decomposition of organic matter in soils rich in lime is more rapid than in soils with a low lime content.

The ammonia nitrogen content of the composts in the carbon dioxide series was determined at the end of 3 weeks, when the experiment was discontinued. At 7°, more than 60 per cent of the ammonia was recovered; at higher temperatures, the greater part of the added nitrogen had been transformed into

organic compounds, and only a small fraction of the inorganic nitrogen was left, less in the presence of CaCO_3 due to greater decomposition and, therefore, greater assimilation of the nitrogen by the microorganisms. This is seen in a comparison between the curves for ammonia assimilation with the corresponding CO_2 curves. In this connection, another interesting fact should be reported here, namely, that the ammonia content of the composts kept at 37° without nutrients has risen to 4.88 mgm. (for 2 gm. of material), whereas at 27° only 0.76 mgm. and at 7° 0.86 mgm. have been found. The latter figures may be due largely to analytical errors, while the former figure indicates definitely that at the higher temperature, decomposition was very rapid and resulted in the liberation of some of the nitrogen in an available form.

In order to understand the complex relations involved in the decomposition of fresh plant materials by microorganisms, a more detailed analysis is presented here concerning the influence of temperature upon the decomposition of the various chemical constituents of oat straw, in the presence and absence of added nutrient salts, as outlined in the first experiment.

INFLUENCE OF TEMPERATURE UPON THE DECOMPOSITION OF THE CHEMICAL CONSTITUENTS OF OAT STRAW

Influence on the Transformation of Ether-soluble Substances

The fatty and waxy substances were extracted from the composts, at different stages of decomposition, with ether and determined quantitatively. These substances form frequently a protective coating around the cell constituents, thus retarding their decomposition. In all the experiments the disappearance of these substances was very much increased with temperature, nearly 3 times as much being decomposed at 37° as at 18° , whereas the de-

TABLE VIII. *Influence of temperature upon the decomposition of ether-soluble (fatty and waxy) substances*

Per cent of complexes left †

Temperature of incubation	Moisture content	Days of decomposition			
		16	48	105	273
7°C.^*	66.6	—	—	80.6	78.9
7°C.	66.6	—	—	93.6	79.4
7°C.	80.0	—	—	71.5	61.1
18°C.	66.6	94.6	90.3	32.1	14.8
18°C.	80.0	96.7	77.3	23.0	14.8
27°C.^*	66.6	—	62.5	35.2	20.8
27°C.	66.6	90.2	—	18.7	13.9
27°C.	80.0	78.6	18.7	10.4	4.8
37°C.^*	66.6	—	33.6	17.8	10.0
37°C.	66.6	33.9	17.4	9.6	6.5
37°C.	80.0	40.0	31.7	4.8	4.3

† On the basis of total concentration in original material.

* Composts without nutrient salts.

composition at 7° was very slow, nearly 80 per cent being still present in two of the samples after 273 days, as shown in Table VIII. It is evident that of all the chemical constituents of the straw the influence of temperature upon the decomposition processes was most pronounced in the case of the fatty and waxy substances (Fig. 6).

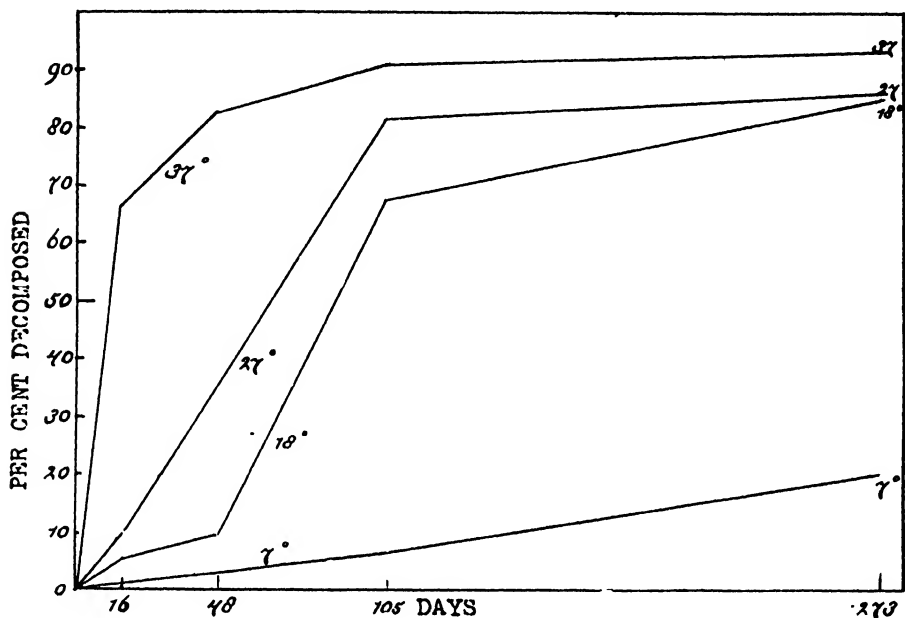


FIG. 6. Influence of temperature upon the decomposition of ether-soluble substances (fats, waxes) in oat straw.

The marked delay in decomposition at 18° is followed by a rapid increase after 48 days. This shows that active organisms were present in the original soil infusion only in small numbers; they multiply slowly at this temperature, but are later able to attack these substances very vigorously. At 37°, the fatty and waxy substances have decomposed at first very rapidly; after 105 days, however, decomposition became very slow. This shows that the straw must contain a small quantity of highly resistant substances among the ether-soluble complexes, which are able to resist decomposition even under optimum conditions. The influence of temperature on the process seems to be of greater importance than the influence of the addition of nutrients: at 18°, with nutrients and 66.6 per cent moisture, only 9.7 per cent has been decomposed after 48 days, while at 27°, without nutrients, 37.5 per cent has disappeared within the same time. Increased moisture content generally favored decomposition.

Influence on the Transformation of Water-soluble Substances

Since microorganisms constantly transform insoluble organic matter into soluble substances, it becomes evident that the amount of water-soluble complexes found in the composts after 105 days consists only partly of the material originally present in the straw and partly of newly formed substances. This is also the reason why, at 37°, 112.1 per cent of hot water soluble substances is found after 16 days, and at 27°, 120.5 per cent. Even without the nutrient salts, there is an increase of nearly 4 per cent during the first 48 days of decomposition. The cold water soluble substances do not show any increase, probably due to the fact that they are more rapidly decomposed than the former. The influence of temperature is not so marked as in the case of other complexes. After 16 days, 62.2 per cent of the original amount was recovered at 18° and 63.4 per cent at 37° (Table IX).

In all cases the quantities of hot water soluble substances left at the end of the decomposition were nearly twice as large as the corresponding amounts

TABLE IX. *Influence of temperature upon the decomposition of cold water soluble and hot water soluble substances*

Per cent of complexes left †

A. *Cold water soluble substances*

Temperature of incubation	Moisture content	Days of decomposition		
		16	48	105
7° C.*.....	66.6	—	—	62.0
7° C.....	66.6	—	—	53.1
7° C.....	80.0	—	—	45.1
18° C.....	66.6	83.5	41.9	36.4
18° C.....	80.0	62.2	44.6	33.2
27° C*.....	66.6	—	80.5	36.4
27° C.....	66.6	46.2	35.0	22.0
27° C.....	80.0	47.5	38.7	28.1
37° C.*.....	66.6	—	53.6	30.4
37° C.....	66.6	46.1	31.4	23.9
37° C.....	80.0	63.4	34.9	28.1

B. *Hot water soluble substances*

7° C.*.....	66.6	—	—	66.5
7° C.....	66.6	—	—	83.0
7° C.....	80.0	—	—	66.9
18° C.....	66.6	90.0	80.1	62.9
18° C.....	80.0	87.6	79.1	65.4
27° C.*.....	66.6	—	103.9	84.8
27° C.....	66.6	120.5	68.8	55.6
27° C.....	80.0	83.4	59.1	47.7
37° C.*.....	66.6	—	65.0	61.0
37° C.....	66.6	112.1	94.6	58.1
37° C.....	80.0	88.7	74.1	71.7

† On the basis of total concentration in original material.

* Composts without nutrient salts.

of cold water soluble substances, because the first seem to be more resistant than the latter.

In view of the fact that, under natural soil conditions, these water-soluble substances will be drained and quickly removed, the results obtained in these experiments are not applicable to the soil without modification.

Influence of Temperature upon the Transformation of Alcohol-soluble Substances

The concentration of substances in oat straw which dissolve in hot alcohol but not in ether or water (extraction following these two treatments), was rather limited, namely, 1.76 per cent. During the early stages of decomposi-

TABLE X. *Influence of temperature upon the decomposition of alcohol-soluble substances*
Per cent of complexes left †

Temperature of incubation	Moisture content	Days of decomposition		
		16	48	105
7° C.*.....	66.6	—	—	102.2
7° C.....	66.6	—	—	126.0
7° C.....	80.0	—	—	109.4
18° C.....	66.6	135.2	92.5	74.0
18° C.....	80.0	127.6	77.3	62.1
27° C.*.....	66.6	—	78.1	64.4
27° C.....	66.6	130.4	83.4	61.1
27° C.....	80.0	104.0	45.1	50.2
37° C.*.....	66.6	—	50.7	40.3
37° C.....	66.6	73.4	47.0	54.0
37° C.....	80.0	85.7	39.8	37.0

† On the basis of total concentration in original material.

* Composts without nutrient salts.

tion (Table X), considerable quantities of alcohol-soluble complexes are produced, either by the microorganisms themselves, through their synthesizing activities, or are set free by the destruction of the cell wall. These substances decompose slowly: in 9 out of 13 cases more than 50 per cent was left after 105 days' decomposition. A higher moisture content increases the rate of decomposition only to a limited extent; the presence or absence of nutrient salts did not seem to have any influence at all upon the decomposition of the alcohol-soluble complexes.

Influence of Temperature upon the Transformation of Hemicelluloses and Cellulose

As the hemicelluloses and cellulose constitute more than 50 per cent of the original material and usually form the greater part of all plant residues which undergo decomposition in nature, the behavior of these substances in the decomposition of plant materials deserves special attention (Tables XI

and XII). The influence of temperature is very marked upon the decomposition of both groups of complexes; at 7°, the decomposition of the hemicelluloses is much slower than that of the cellulose; after 273 days, 20 per cent more of the first group is left than of the second.

TABLE XI. *Influence of temperature upon the decomposition of total hemicelluloses in oat straw*
Per cent of complexes left †

Temperature of incubation	Moisture content	Days of decomposition			
		16	48	105	273
7° C.*.....	66.6	—	—	110.0	83.8
7° C.....	66.6	—	—	89.4	60.5
7° C.....	80.0	—	—	70.0	58.0
18° C.....	66.6	81.6	50.4	32.4	19.1
18° C.....	80.0	84.4	52.2	27.3	24.5
27° C.*.....	66.6	—	70.8	54.0	28.5
27° C.....	66.6	54.5	35.3	23.8	19.2
27° C.....	80.0	56.9	29.6	18.9	11.0
37° C.*.....	66.6	—	74.5	49.1	31.2
37° C.....	66.6	52.8	34.2	16.2	8.2
37° C.....	80.0	51.8	18.3	12.1	5.7

† On the basis of total concentration in original material.

* Composts without nutrient salts.

TABLE XII. *Influence of temperature upon the decomposition of cellulose in oat straw*
Per cent of cellulose left †

Temperature of incubation	Moisture content	Days of decomposition			
		16	48	105	273
7° C.*.....	66.6	—	—	86.8	62.7
7° C.....	66.6	—	—	62.8	38.8
7° C.....	80.0	—	—	50.2	33.1
18° C.....	66.6	60.4	26.2	18.0	6.6
18° C.....	80.0	68.5	25.7	14.5	12.5
27° C.*.....	66.6	—	49.9	34.5	16.9
27° C.....	66.6	38.8	17.5	12.6	10.3
27° C.....	80.0	41.1	14.4	7.2	2.7
37° C.*.....	66.6	—	54.7	38.8	26.0
37° C.....	66.6	46.7	21.6	11.6	7.0
37° C.....	80.0	40.1	6.6	5.4	1.7

† On the basis of total concentration in original material.

* Composts without nutrient salts.

It is important to point out that at 7° without nutrient salts there is evident even a slight increase of the hemicelluloses, possibly due to the synthesis of the fungus mycelium which is known to be rich in hemicelluloses.

A rise of temperature of 11 degrees increased the decomposition processes, especially of the cellulose; after 105 days, there was left twice as much of the hemicellulose group as of the cellulose. At temperatures between 18°

and 37°, the rate of decomposition was the greatest during the first 48 days, at least 50 per cent of the hemicelluloses and 74 per cent of the cellulose having disappeared. On examining figs. 7 and 8 we find that the curves

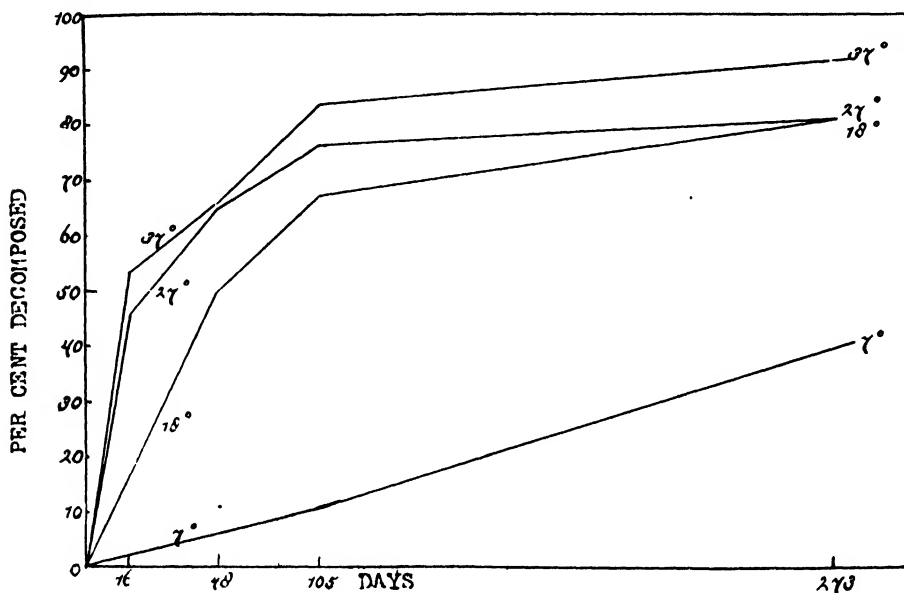


FIG. 7. Influence of temperature upon the decomposition of hemicelluloses in oat straw.

for hemicellulose decomposition show great resemblance to those of cellulose decomposition; only the rate of decomposition of the first is somewhat less, and the optimum temperature seems to be lower for the latter. The cellulose curve of 37° falls between that of 27° and of 18°, which indicates that the optimum temperature for cellulose decomposition is much wider than for the hemicelluloses.

The addition of nutrient salts has had a great influence on the decomposition of the hemicelluloses; this is very striking at 37°, where 31.2 per cent is left after 273 days without nutrients and 8.2 per cent in the presence of nutrients. The cellulose behaved in a similar manner.

The effect of adding available nutrient salts is much more striking at lower temperatures than at higher. The addition of nutrients to the composts kept at 7° results in a much more rapid decomposition, 23.9 per cent more cellulose being decomposed after 273 days with nutrients than without. At higher temperatures the difference is not so striking.

These results tend to prove that the *carbon nitrogen ratio for the optimum decomposition of the cellulose decreases when the temperature is lowered*. This means that with the same or even with a lower amount of nitrogen larger quantities of cellulose can be decomposed when the temperature is raised. The explanation of this phenomenon is found in the fact that at higher tem-

perature the microorganisms live, die and decompose much more rapidly than at lower temperatures, and the nitrogen is changed more rapidly within the microbiological cycle.

The greater resistance of some of the hemicelluloses to decomposition can also be confirmed by experiments on the nature of organic matter decomposed under natural conditions in soil and in peat bogs. An analysis of organic matter in soil from 6 different sources gave concentrations of cellulose varying from 5.2 to 2.8 per cent with an average of 3.8 per cent of the total organic matter. The average for the hemicelluloses was 7.8 per cent (Waks-

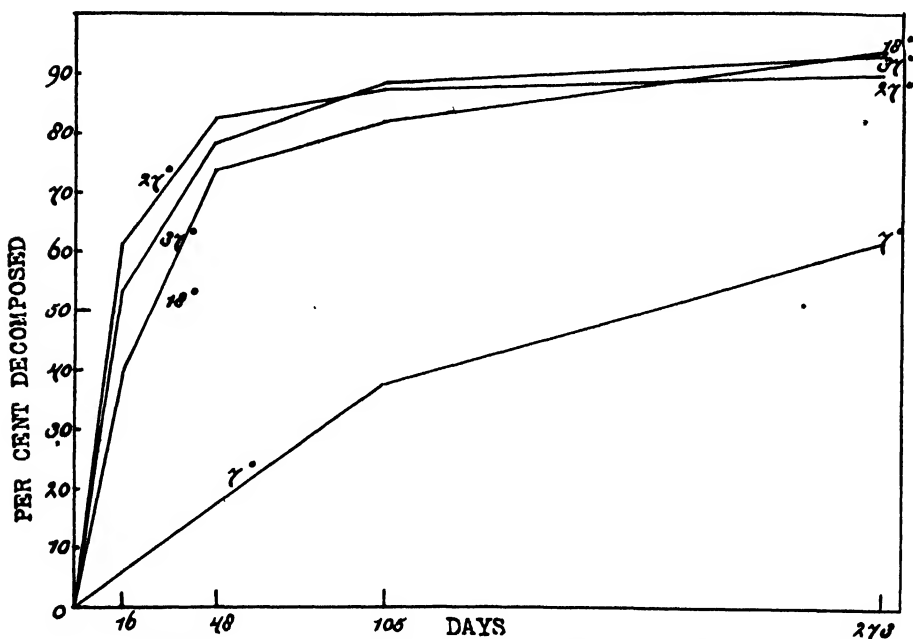


FIG. 8. Influence of temperature upon the decomposition of cellulose in oat straw.

man, '29). When one compares this with the chemical composition of a number of undecomposed plant materials of different origin, one can see that the average cellulose content is 24.9 per cent and that of the hemicelluloses 17.1 per cent (Waksman and Tenney, '27). From these figures one may conclude that although cellulose is much more abundant than hemicelluloses in the fresh materials, the relation is reversed in soil organic matter.

Influence of Temperature upon the Decomposition of Lignins

From the point of view of practical agriculture those components which possess the greatest resistance to decomposition, and have therefore a beneficial effect upon soil fertility by increasing the content of organic matter in the soil, are of the greatest interest. It has been shown that of all the chemical constituents of plant residues added to the soil, the lignins are most re-

sistant to decomposition. They become, in a modified form, an integral part of the soil organic matter, or the so-called "humus complexes" of the soil. As such they deserve our special attention, notwithstanding the fact that their chemical composition is still a matter of dispute. They are characterized by their "insolubility in concentrated mineral acids, solubility in alkalis, high carbon content, etc." In some cases, as a result of the decomposition of the oat straw, there was an actual increase in the total lignin content, especially at the lower temperatures. Whether this is due to an actual synthesis of lignin-like complexes by microorganisms, still remains to be determined. There was little difference between the results of the experiments at 18° and 27° (Table XIII). The rate of decomposition is rather slow at these tem-

TABLE XIII. *Influence of temperature upon the decomposition of lignins in oat straw*
Per cent of complexes left †

Temperature of incubation	Moisture content	Days of decomposition			
		16	48	105	273
7° C.*.....	66.6	—	—	108.2	96.0
7° C.....	66.6	—	—	115.1	102.0
7° C.....	80.0	—	—	94.0	104.4
18° C.....	66.6	103.0	99.2	97.5	85.7
18° C.....	80.0	110.0	99.5	72.5	86.5
27° C.*.....	66.6	—	84.5	83.2	71.6
27° C.....	66.6	103.9	93.5	90.7	88.2
27° C.....	80.0	101.9	85.3	82.9	78.0
37° C.*.....	66.6	—	89.1	62.1	69.0
37° C.....	66.6	100.9	85.9	68.6	54.0
37° C.....	80.0	86.5	76.4	49.7	41.6

† On the basis of total concentration in original material.

* Composts without nutrient salts.

peratures (Fig. 9); after 9 months, not more than 14 per cent of the lignin had disappeared at 18°. At 37°, decomposition of the lignins was most rapid, 30 to 50 per cent of the original amount having disappeared within the first three and one-half months. After that, the rate of decomposition seems to have decreased markedly. This rapidly decreasing rate of decomposition points further to the greater resistance of these complexes as compared with the cellulose and hemicelluloses (Table XIII).

As to the influence of nutrients upon lignin decomposition, one finds here again an entirely different relation from that of the polysaccharides; namely, nutrient salts had practically no effect upon the decomposition of the lignins. In the absence of nutrients, actually smaller amounts of lignins were left at 7° and 27°. Whether this is due to an actual greater lignin decomposition or to the building up of lignin-like complexes by the microorganisms in the presence of nutrients (since considerably more cell substance was synthesized under these conditions, as shown by nitrogen consumption) also remains open

for further investigation. When the amount of lignin left after 1 year of decomposition was determined, it was found that at least 38 per cent of the original amount was left even at the higher temperatures.

A more detailed study of the production and decomposition of lignin and possible synthesis of lignin-like complexes would be of considerable practical

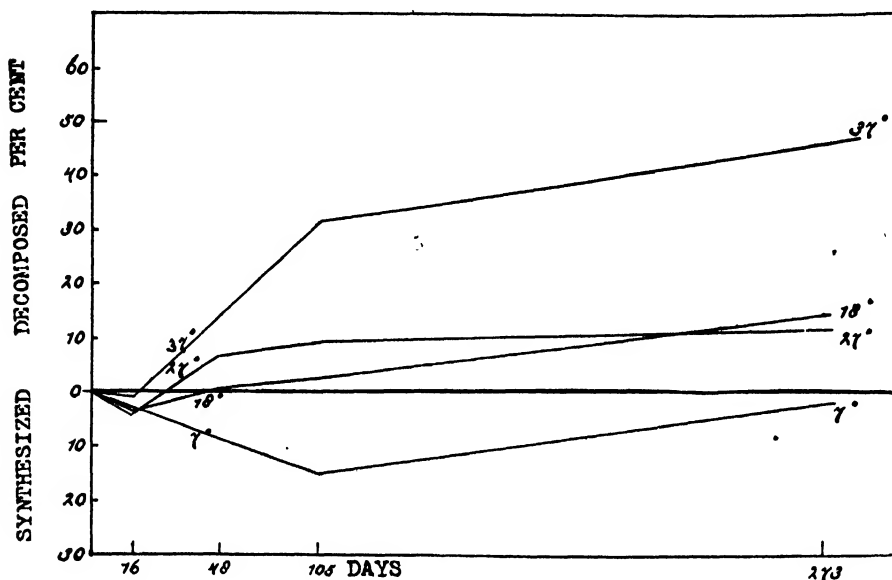


FIG. 9. Influence of temperature upon the decomposition of the lignins in oat straw.

value in enabling us to control the processes of decomposition of organic matter in such a way that a maximum amount of highly resistant "lignin-humus" complexes could be formed under certain conditions, and decomposed under others.

Influence of Temperature upon the Transformation of Nitrogen Complexes

From a practical point of view the proteins and other organic nitrogenous complexes form one of the most important groups of constituents of the soil organic matter, because they represent the nitrogen storage for the growth of cultivated and uncultivated plants. As seen above, processes of synthesis always accompany decomposition of organic matter, the enormous increase in the protein content of the residual material, which in many cases exceeds two to three times that of the protein in the original material (Table XIV) is of great economic importance. As one would expect, the ammonia nitrogen (not shown in Table XIV) rapidly decreased as soon as protein synthesis began. Out of the 1,060 mgm. of nitrogen added to the composts in the form of ammonium salt, 90 per cent or more had disappeared, in most cases within the first 16 days of decomposition.

TABLE XIV. *Influence of temperature upon the transformation of organic nitrogen complexes (proteins), in the decomposition of oat straw*

Per cent of complex left †

Temperature of incubation	Moisture content	Days of decomposition			
		16	48	105	273
7° C.*	66.6	—	—	85.1	131.9
7° C.	66.6	—	—	375.6	313.0
7° C.	80.0	—	—	331.0	
18° C.	66.6	151.9	296.4	347.0	276.0
18° C.	80.0	149.4	309.0	267.8	
27° C.*	66.6	—	78.5	105.1	106.0
27° C.	66.6	250.6	314.2	313.8	240.0
27° C.	80.0	264.0	298.8	229.0	
37° C.*	66.6	—	118.1	119.1	121.8
37° C.	66.6	279.0	304.6	309.8	250.0
37° C.	80.0	240.0	310.0	256.0	

† On the basis of total concentration in original material.

* Composts without nutrient salts.

In one instance, namely, at 37° with 80 per cent moisture, 3 per cent of the original ammonia nitrogen could be recovered after 48 days; 57 days later the proteins began to decrease and the ammonia nitrogen increased to 7.9 per cent of the original amount. At the incubation temperature of 18° and 80 per cent moisture, nearly all ammonia nitrogen disappeared rapidly, with only 1.2 per cent left after 48 days of decomposition. Soon after, however, the proteins began to decompose, decreasing from 309.0 per cent to 267.8 per cent and the ammonia content increasing to 7.9 per cent. The protein curves, the vertical scale of which is only one-third that in the other graphs, bring out some interesting facts (Fig. 10). Protein formation has been most rapid at 37°, the curve for the 27° compost following very closely that for 37°.

It is surprising to note that the largest amount of protein has actually been produced at 7°, reaching 275.2 per cent of the original concentration, notwithstanding the fact that the rate of production (the gradient of the curve towards the horizontal axis) is the smallest. It is evident that this is only possible because protein synthesis predominates over protein decomposition at lower temperatures, while at higher temperatures protein decomposition by microorganisms predominates over protein synthesis after the first stages of active decomposition.

After 105 days' incubation, another remarkable fact can be observed, namely, that the rate of decomposition (in fact the resultant of both synthesis and decomposition) is the same at all temperatures, the curves nearly running parallel (Fig. 10). The effect of adding nutrient salts is far greater in this respect than in the transformation of any other of the chemical constituents; in some cases nearly three times as much protein was formed in the presence of nutrients as without.

An examination of the curves for the composts not receiving any inorganic

nutrients will reveal a decrease in protein content at the beginning of decomposition, which at 27° changes into protein synthesis after 48 days, and at 7° after 105 days. The original material contained considerable quantities of water soluble nitrogenous substances, and it seems that these had to be decomposed first and their nitrogen liberated, before any protein (water insoluble) synthesis could take place. As shown previously, decomposition has been greatly accelerated by an increase in temperature and has been so rapid at 37° and so closely followed by synthesis, that no decomposition can be detected at that temperature. The 27° and 37° curves run parallel to the hori-

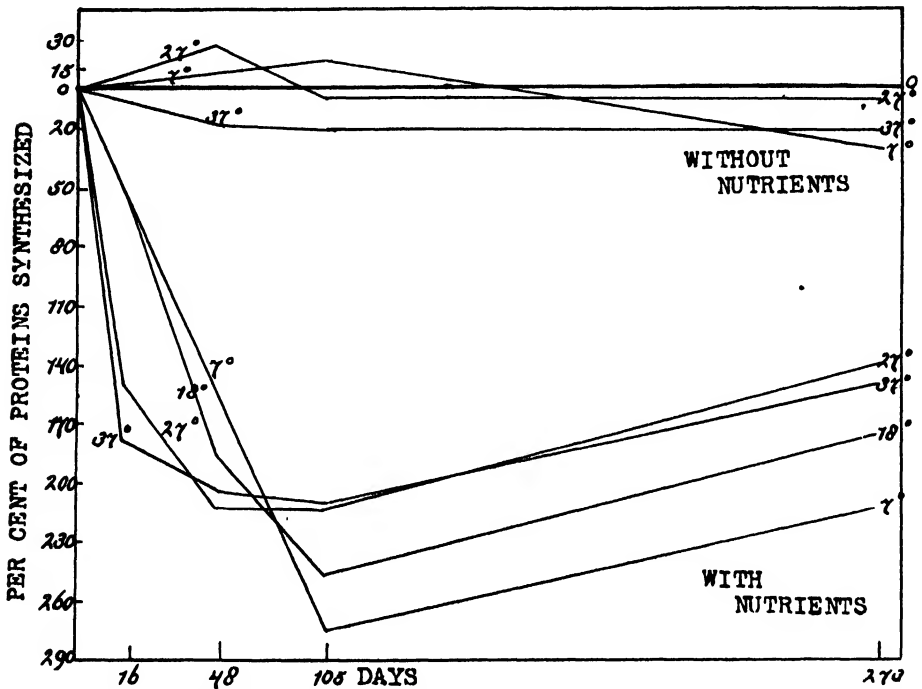


FIG. 10. Influence of temperature upon the decomposition (above horizontal axis) and synthesis (below horizontal axis) of the organic nitrogenous complexes (proteins) in oat straw.

zontal axis for more than 160 days, which shows that no nitrogen is liberated during that time. An examination of the curves of protein transformation in the composts with added nitrogen brings out a marked bending towards the horizontal axis, which proves that protein nitrogen is being transformed into amino and ammonia nitrogen.

These results lead one to conclude that the wider the carbon-nitrogen ratio of a compost, the longer it will take before the nitrogen originally present in the material is liberated and becomes available outside the microbiological cycle. These experiments emphasize the well known fact that by the addition of undecomposed organic matter to the soil, the available nitrogen is nearly

completely removed from solution for a period of several months, even at tropical temperatures.

These facts provide a means of preventing losses of available nitrogen by leaching in those cases where the soil contains more nitrogen than the plants can assimilate. This is sometimes the case after the application of legumes as green-manures; the intelligent use of moderate quantities of chopped straw might not only save the first crop from being overfed with nitrogen, but the nitrogen surplus will also be stored away for the next crop as insoluble proteins, as has been suggested by Sievers and Holtz ('28).

Summary

The results presented in this paper deal with the decomposition of fresh plant material, in the form of oat straw, and of the major groups of its chemical constituents, under the influence of temperature.

The higher the temperature, the more rapid is the decomposition of the plant material as a whole, and of the ether-soluble substances, the hemicelluloses and cellulose.

The influence of temperature is especially marked upon the decomposition of the lignins. At 37°, the lignins are decomposed fairly rapidly; 50 to 60 per cent having disappeared in 9 months. This is not as rapid as the decomposition of the cellulose, but is rather marked. At 7°, however, the lignins are nearly preserved.

The addition of available nitrogen greatly hastens the decomposition of the plant material as a whole and especially of the hemicelluloses and cellulose. It has very little effect, however, upon the decomposition of the lignins.

The lower temperatures favor the synthesizing activities of the microorganisms, while the higher temperatures are more favorable to the organisms bringing about the decomposition processes.

The slower decomposition of the organic matter as a whole and the high carbon content of the lignins fully explain the wider carbon-nitrogen ratio of the organic matter in soils of colder regions as compared with soils of warmer climates.

The predominance of the synthetic over the decomposing processes at lower temperatures find special application in the case of the proteins. As a result of this, the organic matter or "humus" in soils of colder regions should be expected to contain more nitrogen than the organic matter in soils of warmer regions.

The authors are indebted to Mr. H. W. Reuszer for assistance in making the final analyses.

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A THIRD EXPEDITION TO GLACIER BAY, ALASKA

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I. Introduction

In 1916 I made my first visit to Glacier Bay, finding there a region rich in opportunities for research bearing upon the fundamental problems of plant succession. During this visit I made a general survey, and established and charted 9 permanent quadrats in pioneer localities for exact study of successional phenomena. I also made observations upon the relics of interglacial forest which are such a unique feature of the region. A second expedition took place in 1921. The quadrats were recharted, and a careful study was made of the interglacial forest remnants. The results of these two visits are given in detail in an earlier number of this periodical (Cooper, '23).

At the Boston meeting of the Ecological Society of America, in December, 1922, a movement was initiated to have the Glacier Bay region set aside as a national monument. The campaign reached a successful conclusion when President Coolidge, on February 26, 1925, issued a proclamation to that effect (Committee on Glacier Bay, '25).

In beginning the study I had hoped to revisit Glacier Bay every 5 years for the special purpose of recharting the permanent quadrats at regular intervals. It proved impossible to make the hoped-for trip in 1926, and the second interval lengthened to 8 years. In the summer of 1929 a very successful third expedition took place. The party consisted of Miss Frances E. Andrews of Minneapolis, Minnesota, Mr. Chester Roys of Moline, Illinois, Mrs. W. S. Cooper and the author. Sixteen days were spent in Glacier Bay, from July 9 to 24. The quadrats were again charted, new remains of interglacial forest were discovered and studied, and new data obtained bearing upon certain phases of the successional process. A special effort was made to obtain as complete a collection as possible of the flora of the region. Other localities were visited—the Stikine River from Wrangell to Telegraph Creek, B. C., Holkham Bay, near Juneau, and the Davidson Glacier, on the west side of Lynn Canal. The last-named proved to be of very great value for the study of forest development after glacial retreat. A considerable body of data was collected here, but the results are as yet too incomplete for publication. Two other articles based upon the expedition of 1929 are in press (see Literature Cited).

For information regarding the geography and geology of the Glacier Bay region the reader is referred to my first paper (Cooper, '23); a bibliography

of earlier publications is appended thereto. The following brief sketch is provided for those to whom that paper is unavailable.

Glacier Bay is a complex fiord tributary to Icy Strait, 50 miles west of Juneau. Its greatest length is 60 miles. The lower portion is bounded by flat forelands and mountains of moderate height, and contains many islands of till and outwash. Next comes an open expanse 15 miles long and 10 wide, surrounded by abrupt mountain slopes reaching an altitude of more than 5,000 feet. Northward, the bay is divided into two main branches, Muir Inlet on the east, and the upper bay, or northwest arm, on the west. The latter is further subdivided, the various inlets being shown on the map (Fig. 1). The

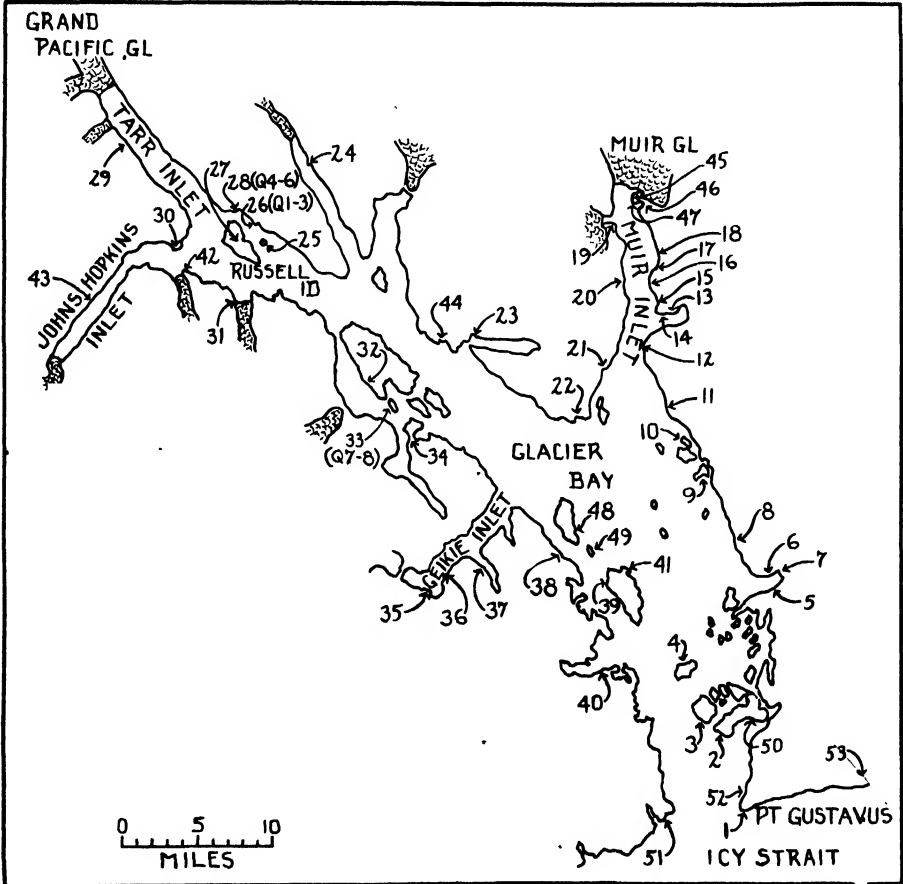


FIG. 1. Map of Glacier Bay, showing the principal geographic features, the location of all stations visited and of the permanent quadrats.

northwest arm cuts deeply into the heart of the Fairweather Range, and the bounding walls of some of its branches attain altitudes of 8,000 to 10,000 feet. A multitude of glaciers of all sorts and sizes descend from the bordering mountains, 10 of them reaching tidewater in 1929.

The known history of the bay begins with heavy glaciation of unknown length followed by a general retreat of considerable magnitude. The period when the shores of

the bay were free from glacial ice, called hereafter "the interglacial period," extended through several centuries. It was brought to a close by an advance, culminating a century and a half ago (possibly somewhat earlier), when the Glacier Bay Glacier discharged directly into Icy Strait. The final event is the present phase of rapid recession, and correlated with this is the contemporaneous vegetational advance which is our principal subject of study. The thing that gives the region its unique value for such investigation is the fact that the retreat is measurable. Vancouver in the narrative of his explorations makes it possible for us to determine the approximate location of the ice front in 1794. John Muir and other later visitors give us very definite information concerning the status of the glaciers at more recent dates. It is thus possible to learn something of the *rate* of succession, a field in which our knowledge is altogether too limited.

I wish to express my appreciation of the generosity of Miss Andrews and Mrs. D. M. Cooper of Minneapolis, who together made possible the expedition of 1929. The cooperation of Miss Andrews as a member of the party contributed a great deal toward the success of the field work. Mr. Roys gave efficient assistance, especially in obtaining increment borings, and Mrs. W. S. Cooper again this year as in 1921. Captain Thomas P. Smith, owner of the gas-boat Yakobi, was in charge of transportation, and his constant interest and cooperation are acknowledged with sincere appreciation. Grateful thanks are extended to the personnel of the Alaskan Aerial Survey, and in particular to Mr. R. H. Sargent and Major Radford, for their service in making a number of aerial photographs in Glacier Bay, two of which are reproduced in this paper.

II. The Present Vegetation Cycle

A. OUTLINE OF THE SUCCESSION

Before describing the supplementary results of the 1929 expedition, some further recapitulation is desirable. The following brief outline of the communities and their developmental relations is accordingly presented.

The vegetation upon the shores of Glacier Bay is disposed in 3 major units: the pioneer community, the willow-alder thicket and the forest. The first is found in scattered fashion in the upper reaches, the second clothes the slopes of the middle bay and the third mantles the mountain sides and lowland surrounding the lower bay.

The process of development which is responsible for the present aspect is briefly as follows. The first arrivals are the mosses *Racomitrium canescens* Brid. and *R. lanuginosum* (Hedw.) Brid., *Epilobium latifolium* L. (broad-leaved willow-herb), *Equisetum variegatum* Schleich. (variegated horsetail) and *Dryas drummondii* Rich. The last is by far the most important because of its mat-forming habit. To some extent with these, and finally surpassing in importance all but *Dryas*, appear 3 species of prostrate willows, *Salix arctica* Pall. being most important. Next comes a group of shrubby willows, *Salix barclayi* And., *S. glauca* L., *S. scouleriana* Barratt, *S. commutata* Bebb, *S. sitchensis* Sans. and *S. alaxensis* (And.) Coville. These usually begin life in depressed or prostrate form, later developing an erect habit, thus constitut-

ing the transition from pioneer to thicket stage. *S. sitchensis* and *S. alaxensis* maintain themselves as important members of the latter community. Alder (*Alnus tenuifolia* Nutt.) gradually asserts itself and becomes the most characteristic thicket dominant. Finally Sitka spruce (*Picea sitchensis* Carr.) supersedes the shrubs, at first forming a pure stand, and to this the two hemlocks, *Tsuga heterophylla* Sarg. and *T. mertensiana* Carr., gradually add themselves.

B. THE PIONEER STAGE

1. Manner and Rate of Initial Invasion

Invaders find environmental conditions most extreme in the various inlets constituting the northwest arm of the bay. The largest of these branches, Tarr Inlet (see map, Fig. 1)¹ is a straight-sided trough 10 miles long and 2 wide, with slopes rising directly from the water's edge to heights of from 5,000 to more than 8,000 feet. Grand Pacific Glacier, which before 1899 completely filled the fiord, now terminates it at its northwest end. In 1916 the slopes of Tarr Inlet were practically bare of plant life. At station 29, 3 miles below the terminus of the Grand Pacific Glacier, careful search revealed some scattered protonema of a moss with a few small sporophytes, and a few diminutive plants of *Epilobium*, mostly starved seedlings less than an inch high. This locality was a fair sample of the whole. Thirteen years later there was evident a very decided greening of the lower slopes in many places. At the 1907 ice-limit and somewhat above, the uneroded gravel remnants showed a covering of vegetation in which *Salix arctica* was probably important. Bearing in mind the many years during which much of the fiord has been ice-free, it is evident that there has been a very considerable lag in the follow-up by plants.

Johns Hopkins Inlet, much narrower than Tarr Inlet, penetrates into the very heart of the Fairweather Range and is bounded for its entire length by tremendously steep walls rising immediately to peaks from 7,000 to 10,000 feet in height. Its trunk glacier, the Johns Hopkins, descends into the southwest extremity, and several other ice tongues cascade steeply over the lateral slopes, two of them reaching sea level. The peaks are loaded with cliff glaciers and névé. In 1907 the Johns Hopkins Glacier front stood at the "elbow." After it had receded around the corner, we have no knowledge of the manner of its retreat until 1926, when W. O. Field ('26), from a high point opposite the elbow, discovered that 8 additional miles of the inlet had been opened up. In 1929 little if any further retreat had occurred. Our party was able for the first time to navigate the waters of this inlet. After threading the ice fields with considerable difficulty we were completely stopped at a point 4 miles from the Johns Hopkins ice cliff. We found the slopes of the lower half of the fiord almost absolutely barren, but at the farthest point

¹ A more detailed map of Glacier Bay is given as the frontispiece to my earlier publication (Cooper, '23, Fig. 1, facing p. 93).

reached there were a few small patches of *Epilobium* in flower, and a small quantity of moss. Comparing those portions of Tarr and Johns Hopkins Inlets which have been vacated by the ice since 1907, the latter is far more barren.

Considering now the advent of the woody pioneers, we have data of a more quantitative sort in a considerable number of age-counts made in the course of the 3 expeditions. In such a study we must take account not only of the prostrate willows but of the shrubby willows, the alder, the cottonwood, and even the spruce, since any of these may sometimes enter as early as the more characteristic pioneers. In the northwest arm 67 age-counts were made, dis-

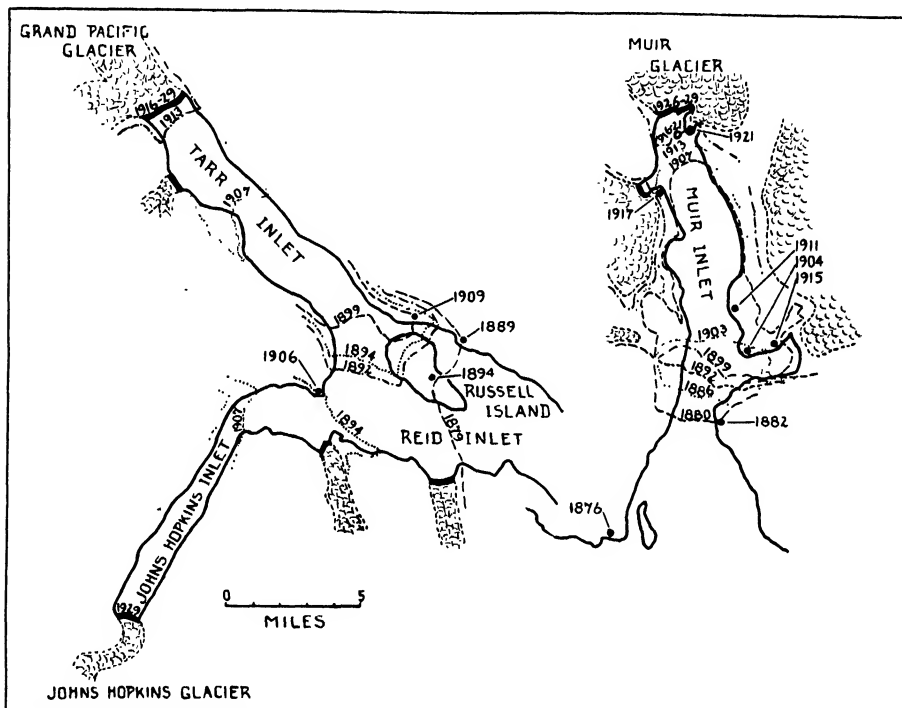


FIG. 2. The northwest arm of Glacier Bay and Muir Inlet, showing the progress of glacial retreat, the year being indicated along the former ice fronts; and the date of arrival of pioneer woody plants, by black dots with lines leading to the years.

tributed among 8 stations. Four of the latter have been selected as significant, and the year of arrival of the oldest woody plant examined at each of these stations has been plotted upon the map (Fig. 2). Three stations are located upon points of accurately known subaerial age, and among these the time intervals between disappearance of ice and arrival of first woody plant are closely similar: 10, 10 and 12 years. The data are scanty, to be sure, but trustworthy so far as they go, for in each station careful search was made over a wide area for the manifestly oldest individuals. Without forcing our data too far we may fairly assume that in this region several years—roughly

a decade—elapsed between disappearance of ice and establishment of the first woody plant.

The map shows that when the ice front in its retreat came to Russell Island, recession became slower for a time, more than 20 years being required for it to pass the rocky mass, which is 3 miles long. After freeing itself of the island, the rate increased greatly, 9 miles being covered in 14 years. Presumably the rate before Russell Island was reached was also comparatively fast. The point where ice recession slowed up for a number of years is also a point of division vegetationally. Below, the gravels are fairly well covered with pioneer vegetation; patches of alder occur and occasional individuals of spruce; while above, we enter the region where vegetation as yet is exceedingly sparse. The evident explanation is that while the ice front was falling back with comparative rapidity through Reid Inlet, plant invasion lagged far behind. The pause at Russell Island permitted the pioneers to catch up and to establish themselves in some quantity to this point. The resumption of rapid recession has been accompanied by a second lag in plant invasion, so that Tarr and Johns Hopkins Inlets show but a scattering of early pioneers and almost no woody plants.

Muir Inlet is approximately equal in size to Tarr Inlet, but is very different in character. It is essentially a sharp depression in a broad lowland, with the mountains in most places standing well back from the shore. Its recent history is indicated on the map (Fig. 2). From 1880 (possibly earlier) to 1903 there was slow retreat, followed by 4 years of extremely rapid recession, 7 miles being covered in this time. Since 1907 the rate has again greatly decreased. The ice upon the bordering lowland has lingered, receding very slowly from the shores of the inlet; the surface open to invasion by plants has thus developed as a narrow strip bounded by water on one side and ice on the other. The follow-up has here been very much more rapid than in the northwest arm. Pioneers have populated the available area in considerable number, following close upon the retreating ice in all directions. Data from age-counts of woody plants demonstrate this conclusively. Using 102 determinations made at 10 points in Muir Inlet, the dates of first arrivals at 7 significant stations have been plotted. Here, in striking contrast to the northwest arm, there is little or no lag in follow-up; the woody pioneers almost tread upon the heels of the receding ice. At the ice limit of 1880 we find an arrival in 1882 (and this invader a spruce!); a pioneer of 1904 almost coincides with the limit of 1903; and one of 1921 stands just outside the line where the ice margin lingered from 1916 to 1921.

Comparison of these 2 contrasting localities suggests the question: what are the hindering factors, differing in intensity in the 2 regions, which govern the rate of follow-up? Environmental conditions affecting plant establishment at once suggest themselves. Some scanty instrumental data obtained in 1921 (Cooper, '23, pp. 229-232) indicate that atmospheric conditions in a given spot become notably ameliorated as the ice margin retreats into the dis-

tance; and yet vegetation, even climax forest, is frequently, elsewhere in Alaska, found extending to the very edge of the ice, and even beyond where it is stagnant and moraine-mantled. Moreover, at Glacier Bay we find the most rapid follow-up in Muir Inlet, where the ice lingers most persistently. The general impression is strong, though unsupported by definite evidence, that conditions governing establishment are at least not the main cause of the differences between Muir Inlet and the northwest arm.

There remains the factor of migration. All the important pioneers have very mobile disseminules—spores in the case of *Racomitrium* and *Equisetum*, plumed seeds or fruits in *Epilobium*, *Dryas* and the willows. Wind, as an agent in migration, might have an important bearing upon the problem, and the fact that the order in which the invading species appear is strictly correlated with the relative mobility of their disseminules renders this hypothesis more plausible. The Glacier Bay region in summer is notably calm. Day after day the surface of the water maintains a mirror-like stillness. Particularly is this true of the thoroughly protected northwest area. During the total of 14 days that I have spent there I have never seen the surface more than mildly rippled. In Muir Inlet, on the other hand, I have occasionally encountered rough water. Such summer breezes as occur in the region are mainly down-glacier currents, unfavorable to migration into new areas. Occasional strong south breezes do occur, however, which might carry disseminules into the upper reaches. Muir Inlet, on a north-south line with the mouth of the bay, is open to these, while the northwest arm is effectively sheltered by the enormous mass of the Fairweather Range.

The fact is certain that invasion follows the ice very closely in Muir Inlet and lags far behind it in the northwest arm. Factors governing establishment do not seem adequate to account for the difference, and wind, as an agent in migration, appears to offer a reasonable explanation.

2. *Permanent Quadrats*

In 1916 I established 9 permanent one-meter-square quadrats in 3 localities on the shores of Glacier Bay, with the intention of recharting them at intervals for as long a period as possible. They were placed at points where the ice limit at certain dates had been definitely located, and thus at points of known subaerial age. The prime purposes were to bring to light the minute events and changes which make up the stream of successional progress, and to discover as much as possible concerning the time factor in development.

The conclusions derived from the first five-year period were presented in my former paper (Cooper, '23, pp. 355–365; map, Fig. 2, p. 99). In 1929 the localities were revisited and the quadrats charted for the third time. Unfortunately one (number 9) had been destroyed since 1921 by erosion of the gravel terrace upon which it was located, and because of this fact it has been necessary to recalculate the data obtained in 1916 and 1921 on the basis of

8 quadrats instead of 9. The situation and history of the quadrats are as follows (see also map, Fig. 1):

Station	Locality	Quadrats	Date of first exposure	Subaerial age in 1916
28	Reid Inlet	4-5-6	1899	17
33	Hugh Miller Inlet	7-8	1892	24
26	Reid Inlet	1-2-3	1879	37

Another modification has been found necessary. Numerical treatment of the mat-forming plants, *Dryas*, *Racomitrium* and *Stercocaulon*, feasible in 1921, proved impossible because of extensive coalescence of units; they are now treated solely according to area. Because of these changes a recapitulation of previous results is unavoidable, and the discussion thus becomes a complete history of the study through the year 1929.

It was my original intention, in placing the 3 groups of quadrats, to institute a comparison of development upon areas of differing subaerial age. The localities proved, however, to be unfortunately situated for such a study. The two groups giving the maximum age difference of 20 years were but 2½ miles apart, in the region where the ice front, supported by the mass of Russell Island, lingered for many years, its influence upon the older station continuing almost as great as upon the younger. When finally free of the close proximity of the ice, the 2 areas were not notably unequal in successional advancement. The 8 surviving quadrats are, therefore, lumped in the present treatment.

The plant population is divided into 3 ecological groups: perennial herbs (including *Arctous alpina*, a prostrate shrub of slight importance), the shrubs (all willows), and the mat-plants. Table I presents statistics as to the perennial herbs, of which 8 species occur in the quadrats. The totals for all species not mat-forming (herbs and willows) are added in the last column. Germination is copious and mortality high, a quick turnover of population resulting. The rapidity of replacement is emphasized by the fewness of survivals through the complete period of 13 years. Of 290 individuals present in 1916, but 20 were alive in 1929, all but one of these being *Equisetum*. The net population showed a loss at the end of each period, but at a decreasing average annual rate. Competition with the mat-plants is one of the causes, but probably not the sole one.

Three species merit special consideration. *Equisetum variegatum* exhibits a net gain at a practically constant rate. Of the original 150 individuals, 19 were surviving in 1929. It is the most persistent of the perennial herbs. *Epilobium latifolium*, always among the first in pioneer localities, was abundant in 1916, had decreased by 91 per cent in 1921, and had practically disappeared in 1929. Only 4 new arrivals had appeared in 1921 and none in 1929. Most of the individuals concerned were depauperate seedlings. This species, though

TABLE I. Perennial herbs on quadrats 1-8, and total population except mal-plants

	<i>Equisetum variegatum</i>	<i>Ephedrium latifolium</i>	<i>Carex sp.</i>	<i>Euphrasia mollis</i>	<i>Poa Alpina</i>	<i>Polytrichum sp.</i>	<i>Habenaria hyperborea</i>	<i>Arcobas alpina</i>	Perennial herbs total	Perennial herbs and Saxif.
1916.....	150	110	27		1		2		290	429
1921.....	78	104	15				2		199	250
Germinations, 1921.....	89	4	31	17	15	2	2	1	161	213
Net gain or loss, 1921.....	161	10	43	17	16	2	2	1	252	392
Net gain or loss, 1921.....	+11	-100	+16	+17	+15	+2		+1	-38	-37
Germinations, average per year.....	15.6	20.8	3.0						39.8	50.0
Net gain or loss, average per year.....	+2.2	-20.0	+3.2						32.2	42.6
Germinations, average per year.....	17.8	0.8	6.2						-7.6	-7.4
Net gain or loss, average per year.....	52.0%	94.6%	55.6%						68.6%	58.2%
Germinations.....	59.3%	3.6%	114.8%						55.5%	49.6%
Net gain or loss.....	+7.3%	-90.9%	+59.2%						-13.1%	-8.6%
1929.....	98	9	39	17	14	1	1		179	274
Germinations, 1929.....	112	1	47	8	3	1	1		171	197
Net total, 1929.....	175	1	51	8	5	1	2	1	244	315
Net gain or loss, 1929.....	+14	-9	+8	-9	-11	-1			-8	-77
Germinations, average per year.....	12.3	1.1	4.9						22.4	34.3
Net gain or loss, average per year.....	14.0	-1.1	5.9						21.4	24.6
Net gain or loss, average per year.....	+1.8	-1.1	+1.0						-1.0	-9.6
Germinations.....	60.8%	90.0%	90.8%						71.1%	69.9%
Net gain or loss.....	69.6%	109.3%	109.3%						67.9%	50.3%
Germinations.....	+8.7%	-90.0%	+18.6%						-3.2%	-19.6%
Surviving, 1916-1929.....	19		1						20	66

TABLE II. *Salix*, all species, on quadrats 1-8

	<i>S. arctica</i>	<i>S. boreloyi</i>	<i>S. sitchensis</i>	<i>S. alaxensis</i>	<i>S. spp.</i>	<i>Salix</i> , total
Total, 1916.....	13	46	29	8	43	139
Mortality, 1921.....	1	26	6		18	51
Germinations, 1921.....	3	17	3		29	52
Net total, 1921.....	15	37	26	8	54	140
Net gain or loss, 1921.....	+2	-9	-3		+11	+1
Mortality, average per year.....	0.2	5.2	1.2		3.6	10.2
Germinations, average per year.....	0.6	3.4	0.6		5.8	10.4
Net gain or loss, average per year.....	+0.4	-1.8	0.6		+2.2	+0.2
% mortality.....	7.7%	56.5%	20.7%		41.8%	36.7%
% germinations.....	23.1%	37.0%	10.3%		67.5%	37.4%
% net gain or loss.....	+15.4%	-19.5%	-10.3%		+25.6%	+0.7%
Mortality, 1929.....	8	22	17	2	46	95
Germinations, 1929.....	3	13	1		9	26
Net total, 1929.....	10	28	10	6	17	71
Net gain or loss, 1929.....	-5	-9	-16	-2	-37	-69
Mortality, average per year.....	1.0	2.8	2.1	0.3	5.8	11.9
Germinations, average per year.....	0.4	1.6	0.1		1.1	3.3
Net gain or loss, average per year.....	-0.6	-1.1	-2.0	0.3	-4.6	-8.6
% mortality.....	53.3%	59.5%	65.4%	25.0%	85.2%	67.8%
% germinations.....	20.0%	35.2%	3.8%		16.7%	18.6%
% gain or loss.....	-33.3%	-24.3%	-61.6%	-25.0%	-68.5%	-49.3%
Surviving, 1916-1929.....	11	12	9	6	8	46

TABLE III. *Salix*, established individuals

	<i>S. arctica</i>	<i>S. borealyi</i>	<i>S. silchensis</i>	<i>S. alaxensis</i>	<i>S.</i> , spp.	<i>Salix</i> , total
Total, 1916.....	2	2	5	1	1	11
Mortality, 1921.....	6	6	11	6	5	34
Seedlings 1916, established 1921.....	-1	2	16	7	1	4
New arrivals, established 1921.....	-9	10	+11	+6	7	49
Net total, 1921.....	+7	+8			+6	+38
Net gain or loss, 1921.....						
Mortality, average per year.....	1.4	1.6	2.2	1.2	1.2	7.6
Additions, average per year.....	+1.4	+1.6	+2.2	+1.2	+1.2	+7.6
Net gain or loss, average per year.....						
Mortality, 1929.....	3	7	10	2	3	18
Seedlings 1921, established 1929.....	2	17	2	5	2	13
New arrivals, established 1929.....	1	9	8	-2	6	1
Net total, 1929.....	9	+7	-8	0.3	-1	45
Net gain or loss, 1929.....						-4.0
Mortality, average per year.....	0.4	0.9	1.3	0.3	0.4	2.3
Additions, average per year.....	0.4	+0.9	-1.0	-0.3	0.3	1.8
Net gain or loss, average per year.....					-0.1	-0.5
Surviving, 1916-1929.....	9	9	8	5	5	36

conspicuous, is of little importance in the successional process. *Carex* sp. (nowhere flowering in the quadrats, but probably *C. incurva* Lightf.) is of frequent occurrence and shows a steady increase throughout the complete period, but general observation does not suggest that it will become of any real importance.

In Table II are set forth statistics relating to the various willows occurring in the quadrats. A slight gain during the period 1916-1921 was followed by a considerable loss during 1921-1929. Even during the first period two species, *S. barclayi* and *S. sitchensis*, sustained serious losses, which were barely counterbalanced by the gains made by other species. During the second period a decrease is recorded for every species. The small number of germinations during the second period is particularly noteworthy. Very naturally the willows are far more persistent than the perennial herbs. Of a total of 139 present in 1916, 88 were surviving in 1921 and 46 in 1929. In the final year 70 per cent of all survivors from 1916 were willows.

In Table III a history is presented of the individual willows which become firmly established, the development of measurable prostrate branches being taken as the criterion of establishment. In 1916, of a total of 139, 11 were well established. In 1921, with no deaths, the number had grown to 49, including the original 11, 34 graduates from the seedling class and 4 new germinations. The count in 1921 showed a mortality of 18 and but 13 accessions, all but one of the latter being graduates from the seedling class. The result was an actual net loss at the rate of 0.5 individual per year. Of the 45 present in 1916 (11 established and 34 future graduates), 36 were surviving in 1929.

Vigor of development of the established individuals has an important bearing upon the successional process. Table IV gives statistics based upon measurements of the length of the prostrate shoots.

TABLE IV. *Aggregate shoot-length of Salix, all species*

	1916	1921	1929
Aggregate shoot-length.....	649.5 cm.	1568.6 cm.	2114.6 cm.
Total increase.....		919.1	546.0
Increase, average per year.....		183.8	68.3

Here at last is definite progress. The increase in the size of the willows is of importance, for the prostrate branches, more or less interlacing, produce and hold organic materials which will nourish future invaders. Again, all of the species except *S. arctica* and *S. stolonifera*, though prostrate in pioneer environment, are potentially erect shrubs. At any time, as conditions become less severe, they may put forth upright branches, thus initiating the thicket stage of the succession. There is a sharp drop in rate of increase during the second period, the annual average being little more than one third of that during the first. In general, the willows are steadily decreasing in number, even those of the established class; the most vigorous of the latter are in-

creasing in size, and are a factor to be reckoned with in future successional progress.

Three common species are definitely mat-plants: *Dryas drummondii*, *Rhacomitrium canescens* (with some *R. lanuginosum*) and *Stereocaulon tomentosum* Fr. Sched. Areal treatment is most appropriate for these, the measurements being easily made upon the quadrat charts by planimeter. Where symbols were formerly used for single plants or small clones, arbitrary areas have now been assigned which fairly approximate the average space covered by the individual plant: *Dryas*, 0.05 sq. dm.; *Rhacomitrium* and *Stereocaulon*, 0.01 sq. dm. Table V presents the facts concerning the 3 mat-plants separately

TABLE V. *Mat-plants: areas separately and combined*

	Area	Increase	Average Annual Increase
<i>Dryas</i> (Q. 1-8)			
1916.....	26.65 sq. dm.		
1921.....	119.50	92.85 sq. dm.	18.57 sq. dm.
1929.....	248.95	129.45	16.18
<i>Dryas</i> (omitting Q: 2)			
1916.....	10.84		
1921.....	20.56	9.72	1.95
1929.....	148.95	128.39	16.05
<i>Rhacomitrium</i>			
1916.....	39.83		
1921.....	51.89	12.06	2.41
1929.....	71.30	19.41	2.43
<i>Stereocaulon</i>			
1916.....	0.45		
1921.....	1.39	0.94	0.19
1929.....	22.35	20.96	2.62
All mat-plants			
1916.....	66.93		
1921.....	187.82	120.89	24.18
1929.....	342.60	154.78	19.35

and combined. *Dryas* is by far the most important. The figures show a constant rapid increase throughout the complete period, at a slightly decreasing rate—which is deceptive, because certain of the arbitrarily limited areas become completely filled and show no more gain, whereas the plants which originated within them continue to spread at an equal or even increasing rate. A truer picture of the progress of *Dryas* is obtained by omitting quadrat 2, almost filled in 1921 and completely so in 1929, and figures thus derived are added in Table V. The acceleration in rate of increase where arbitrary limits are not effective is very great, and general observation provides ample confirmation of the facts obtained from the quadrats. The tremendous increase in area dominated by *Dryas* is the most striking fact in the whole history.

The moss, *Rhacomitrium*, has maintained a constant moderate increase,

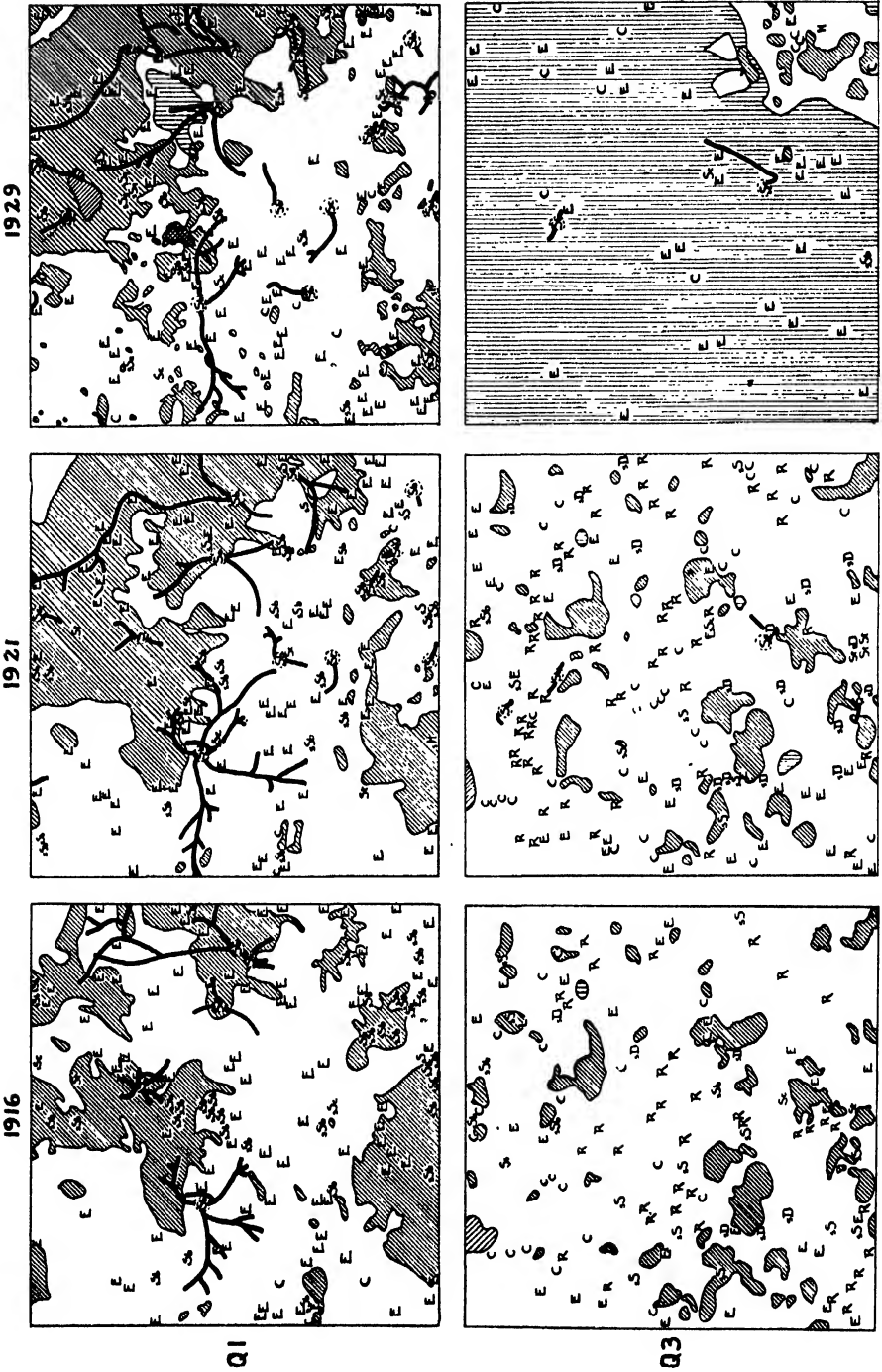


FIG. 3. Quadrats 1 and 3: charts made in 1916, 1921 and 1929. For key to symbols see figure 5.

with little difference in rate, throughout the complete period. It is of considerable importance in the earliest stages, but has no chance of survival in competition with *Dryas*. *Stereocaulon* was insignificant in 1916 and 1921, but had jumped to a position of some consequence by 1929. It, too, is sure to be eliminated in competition with *Dryas*.

Combining the three, we find a large steady increase, due principally to *Dryas*, with the same qualifications by reason of arbitrary limitation of area. Computed as percentage of the total area of 800 sq. dm., we find that the portion covered in 1916 (8.4 per cent) had tripled in 1921 (23.5 per cent) and again almost doubled in 1929 (42.8 per cent), the average annual rate remaining about the same (2.8–3.0 per cent).

The appropriate time has come to put on record in chart form the complete story of the quadrat study, and Figs. 3–6 are accordingly presented. Opportunity is thereby afforded to point out some of the interesting vicissitudes to which the plant population is subject.

Quadrat 1, 1921 (Fig. 3), shows increase and coalescence of areas of *Rhacomitrium* in the upper half and shrinkage in the lower, and a notable gain in aggregate length of willow shoots. The 1929 chart exhibits a decided break-up of the *Rhacomitrium* masses and the death of a considerable portion of the willow branches. *Dryas* makes its first appearance in this area as a small patch whose future history will be followed with interest.

Quadrat 2 is not reproduced here, since its condition in 1916 and in 1921 were presented in the previous paper (Cooper, '23, Fig. 4, p. 358), and no changes of consequence have occurred since the latter date.

Quadrat 3 (Fig. 3) changed very little from 1916 to 1921. Half a dozen seedlings of *Dryas* were present in 1916 and about twice as many in 1921. In 1929, the whole quadrat was found to be covered by a mat of *Dryas*. Only a corner, shaded by a bush of *Lepargyrea* rooted outside the quadrat escaped. The *Dryas* mat may have developed in part from seedlings within the quadrat, but mainly, in all probability, by invasion from without. In competition with *Dryas*, *Rhacomitrium* has disappeared entirely, *Carex* has survived to some extent, and *Equisetum* has remained almost undiminished in number. Two willows, established in 1921, have maintained themselves but with little additional growth; seedling willows have practically disappeared.

Quadrat 4 (Fig. 4) also shows increase of *Dryas*. One area, small in 1916, has greatly enlarged in 1921, and a number of seedlings have appeared. In 1929 more than 50 per cent of the quadrat is covered, and a large area in the region of the old nucleus is over-mature and mostly dead. There is increase in established willows, both in number and extent, and total elimination of *Rhacomitrium*.

In Quadrat 5, 1916 (Fig. 4), a pure growth of *Epilobium* (mostly small seedlings) is replaced in 1921 by abundant sporelings of *Rhacomitrium*, which in 1929 have coalesced, covering large areas. In 1929 there is also a sudden increase in *Stereocaulon* and rapid enlargement of a thrifty arctic willow.

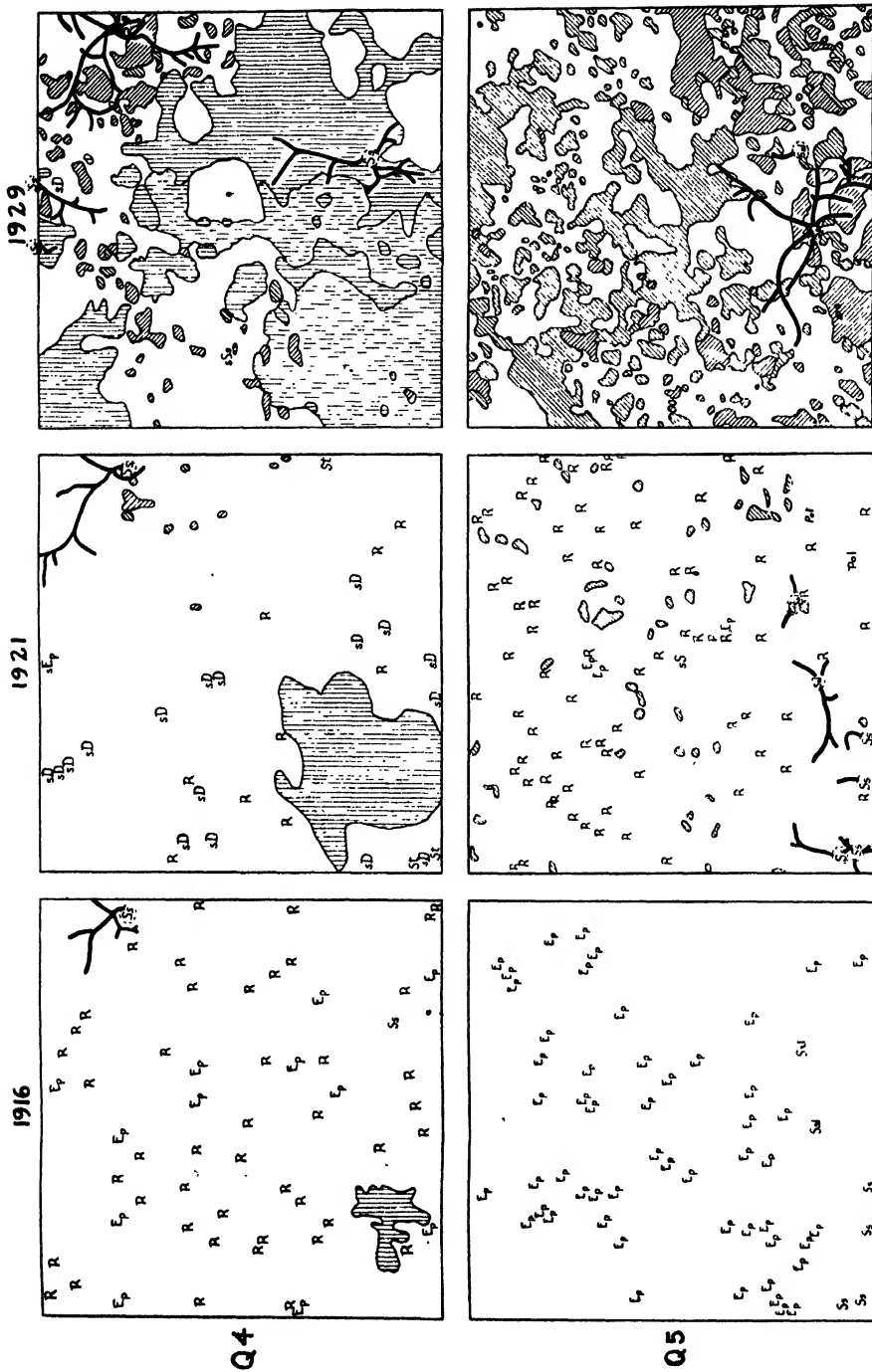


FIG. 4. Quadrats 4 and 5. For key to symbols see figure 5.

In Quadrat 6 (Fig. 5), we again find replacement of *Epilobium* by *Rhacomitrium*, and rapid development of seedlings of Sitka and Barclay willow into established plants. Invasion by *Dryas* from without has begun in 1929.

In Quadrat 7, 1916 (Fig. 6), a multitude of *Dryas* seedlings and some small patches are present, both lessened in 1921. In 1929 we find coalescence of patches together with disappearance of most of the unattached seedlings. An increase in willow development in 1921 is followed by a decrease in 1929.

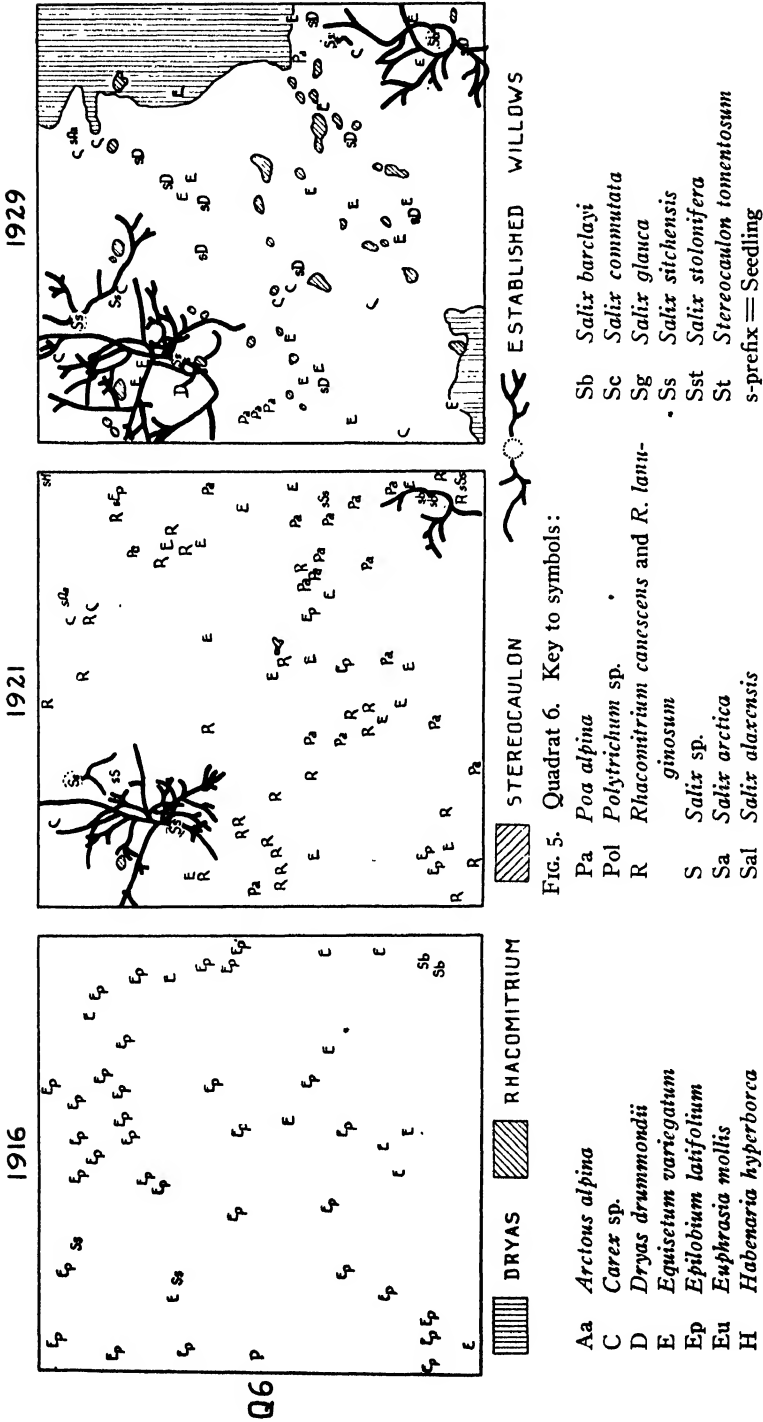
Quadrat 8, 1916 (Fig. 6), shows abundance of willow seedlings, many persisting till 1921 with slight development. Most of them are gone in 1929, but a few have succeeded in establishing themselves. *Dryas* seedlings are present in abundance in 1929.

By way of summary for this quadrat study, Table VI is presented. The

TABLE VI. Average annual net gain or loss on quadrats

	Before 1916	1916-1921	1921-1929
Perennial herbs.....	+17.1	-7.6	- 1.0
<i>Equisetum</i>	+ 8.8	+2.2	+ 1.8
<i>Salix</i>	+ 8.2	+0.2	- 8.6
Established.....	+ 0.6	+7.6	- 0.5
Shoot length.....	+38.2 cm.	+183.8 cm.	+68.3 cm.
Mat-plants (omitting Q. 2)....	+ 2.98 sq. dm.	+4.65 sq. dm.	+21.08 sq. dm.
<i>Dryas</i> (omitting Q. 2)....	+ 0.64	+1.95	+16.05
<i>Rhacomitrium</i> (omitting Q. 2).....	+ 2.31 "	+2.52 "	+ 2.43 "

figures given for the time before 1916 are based on a period of 17 years, the minimum subaerial age of the 3 localities. Naturally every element shows a gain; the figures present merely the net results of a long complex process, of the details of which we know nothing. Evidently this period was characterized by domination by perennial herbs—if we may speak of "domination" in so open a community. *Rhacomitrium*, increasing slightly throughout the complete period, was relatively of greater importance at this early time. Another notable feature of the period before 1916 was the abundant germination of various species of *Salix*. Very few, however, had become established. Mat-plants, though frequent, were insignificant in comparison with their later status. During the second period, 1916-1921, the perennial herbs as a class sustained a loss, though *Equisetum* made a gain at a reduced rate. This time was characterized primarily by the firm establishment of certain of the willows already present. In 1921-1929 the perennial herbs approximately held their own, and the period of willow establishment had evidently come to an end. The individuals most firmly established showed considerable added growth but at a lower rate. The prime feature of the third period is the very great increase of the mat-plants, strikingly shown when quadrat 2 is omitted.



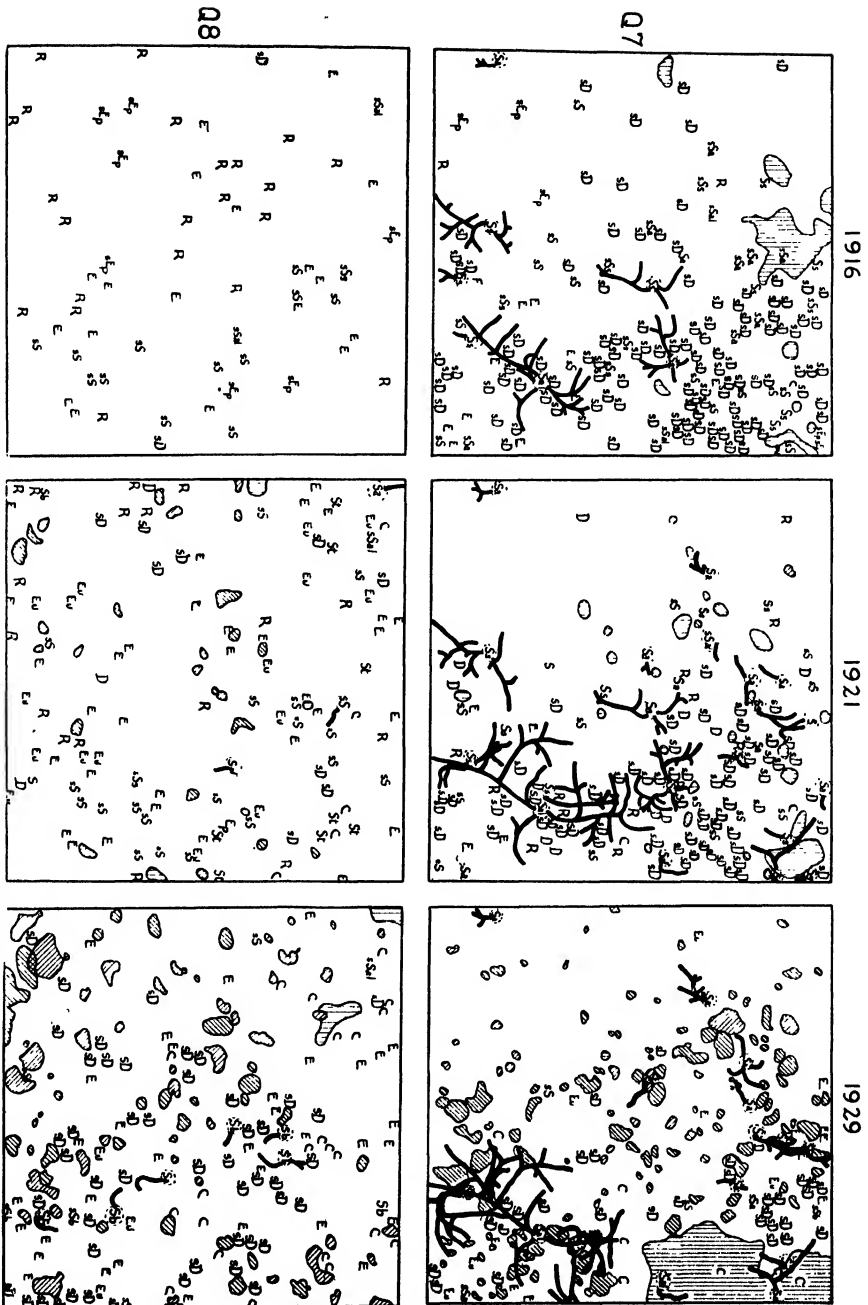


Fig. 6. Quadrats 7 and 8. For key to symbols see figure 5.

In the earlier study, based on the period 1916–1921, a general acceleration was noted in rate of successional advance. During the second period this is not so evident. There has been, in fact, an actual slowing in the progress of certain elements, notably the willows. The mat-plants, however, are so extremely important in humus-producing and humus-holding power that their activity alone may constitute an actual acceleration in successional progress which cannot now be expressed in figures.

In view of the great importance of *Dryas* in the early stages of the succession, a brief sketch of the habits and peculiarities of this interesting and versatile species should be added. Its plumed achenes are admirably adapted to long-distance transportation by wind, and its seeds germinate with great readiness. It is not usually present among the very first invaders, which have still more mobile disseminules, but, once established, rapidly assumes a position of dominance. Developing upon a level surface, with freedom from

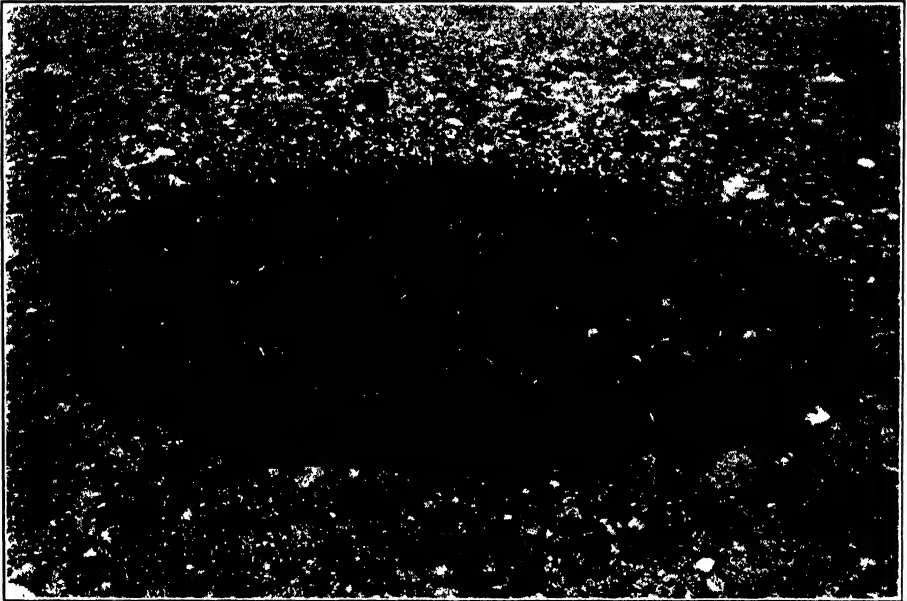


FIG. 7. *Dryas drummondii*: a symmetrical mat developed in a situation free from competition. Station 26.

competition, it forms circular mats of remarkable perfection (Fig. 7). It grows over stones of considerable size, often burying a gravelly flat littered with cobbles beneath an undulating mantle of tangled stems and closely placed yellow-green leaves. Such a development is illustrated in figure 8. When picture A was taken, in 1916, numerous patches of *Dryas* were present, but the area was mainly bare; in 1929 the covering was almost complete. With equal readiness it spreads over smooth glaciated rock ledges, making a firm carpet that may be lifted intact. When gravels supporting a growth of *Dryas*

are undermined by erosion, the tough mat drops down like a curtain over the crumbling surface, offering effective resistance to further removal (Fig. 9). In competition with it, plants of lower stature, such as *Rhacomitrium* and *Stereocaulon*, have no chance; taller species, like *Equisetum*, survive but cannot reproduce. There are indications that its period of dominance is self-

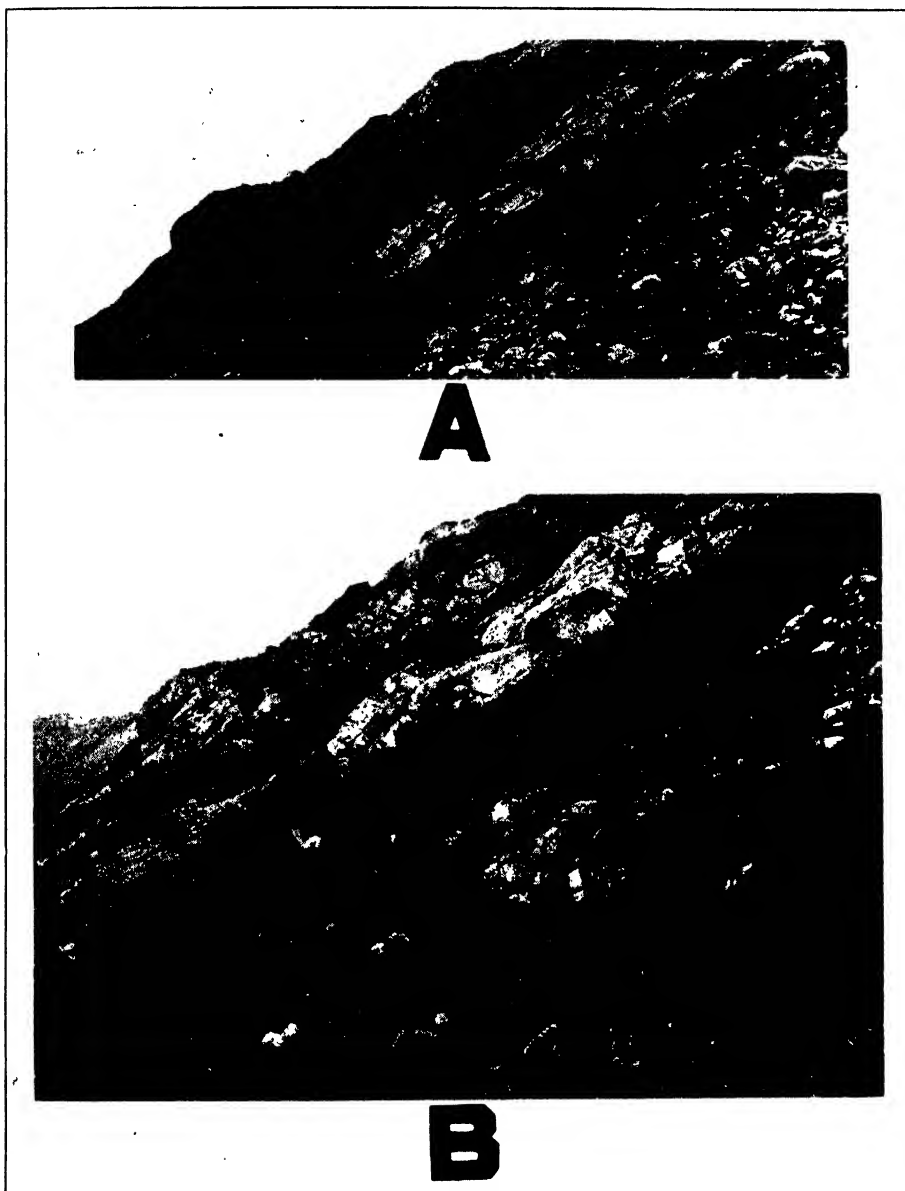


FIG. 8. Successional progress during thirteen years: A, 1916; B, 1929.
Dryas most important. Station 26.

limited. Apparently the older areas become mature and die, the tough masses still remaining as a ground cover. This process has already begun in quadrat 4. *Dryas* is intolerant of shade. Its final doom is fixed by the development into erect bushes of willows of its own generation. Even in areas that have attained no further than the open thicket stage it has usually already disappeared.



FIG. 9. *Dryas drummondii*: a tenacious mat hanging over the edge of a gully, hindering further erosion. Station 26.

C. THE THICKET STAGE

The expedition of 1929 threw considerable new light upon the successional behavior of the alder. This shrub, though it appears sparingly with the earliest pioneers, is characteristically a later arrival. It does not spring up simultaneously in a multitude of places, as do the willows, which fact is doubtless due to the less mobile character of the disseminule. A single individual, germinating in a new locality and becoming established there, becomes a center of local colonization. A small thicket results, which increases in area through short-range but abundant distribution of disseminules. Sometimes these colonies may appear at a considerable distance from the nearest parent areas. An excellent example was observed at station 26 in the northwest arm. Here was an exceedingly dense thicket, half an acre in extent, the tallest central bushes being 12 feet high. There was no sign of it in 1916. In 1929 there

were still no other alders in the vicinity, the nearest being a similar isolated group one-half mile down the shore. Both are shown in figure 10, the second appearing in the far distance.

The thicket which we are describing is composed of 2 partially merging groups. The upper (at the left in the photograph) is the older. It is essentially even-aged, 5 trunks selected at random being 14, 14, 12, 12, 12 years old. It probably represents the closely grouped progeny of a single pioneer which had established itself several years earlier. This individual was not found. The lower group (the right-hand portion of the thicket) centered around a single large individual, plainly visible in figure 10. Its principal branches were contorted and prostrate at base. Being 13 years old, it is of

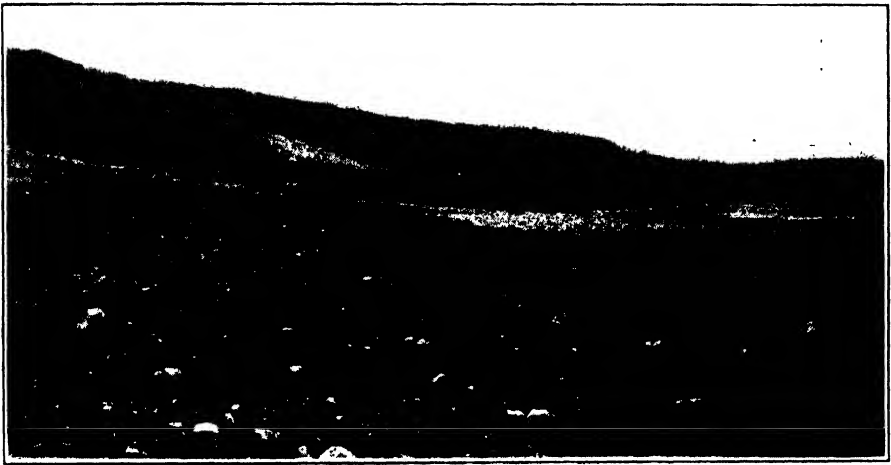


FIG. 10. Pioneer alder thicket at station 26; another in the distance, right.

the same generation as those of the upper group, differing from them in having grown up in the open, free from competition. As a result it is taller than its contemporaries and its branches are much greater in diameter. The average width of ring in one of its stems was found to be 4.77 mm.; the average for the 5 stems selected from the upper group was 2.62 mm. Around this individual were gathered its progeny: scattered medium-sized bushes 10–15 feet apart, with the intervening spaces densely filled with small ones 6–7 feet high, not prostrate at base, and 1–2 inches thick. Four stems selected from the smaller bushes, subject to severe competition, gave ages of 7, 7, 7, 6 years old and an average ring-width of 2.85 mm.—quite comparable to that of the upper group. Occupation of the ground has here attained its limit, and further establishment is possible only outside the thicket, where we find in all directions, to a distance of about 100 feet, a scattering of shrubs ranging from the smallest seedlings to a height of 5 feet. These are open and bushy in habit, with the lower branches prostrate. Five ring counts showed ages of 4, 4, 3, 3, 3 years.

Isolated alder thickets such as this may be seen here and there upon the slopes bordering the northwest arm. While they are increasing in number and size, the immense intervening tracts are growing up to a thicket of willows of various species, in which *Salix sitchensis* and *S. alaxensis* soon obtain the mastery. The result is a mosaic made up of pure stands of willow and of alder, together with various mixtures of the two. In the long run the alder, because of its taller and denser growth, increases its dominance at the expense of the willows, and, were it not for the intervention of the conifers, would undoubtedly supersede the former entirely.

D. THE FOREST STAGE

The spruce requires fairly open conditions for successful invasion. An area of alder, therefore, once established, will maintain its purity for a long period. The willows do not produce so dense a stand, and consequently we find among them a constantly increasing number of young spruces. The willows are soon overtopped by these, and an area of spruce forest is the normal result. Alternation of such groups with areas of pure alder, producing a mosaic pattern, is the logical continuation of the willow-and-alder mosaic described in the preceding section.

Development in this patchwork fashion, however, is but part of the picture. Very often the willow-spruce combination is early invaded by alders through the extension of old colonies and the establishment of new ones. Three elements are now in competition. Of these, the willows are the least able to hold their own, and consequently drop into a state of minor importance. Thus we find great expanses of thicket overwhelmingly dominated by alder, with well-established spruces rising above. Such is the past history of the extensive thickets which cover the shores of the middle bay (Fig. 11). The future history of these areas, clearly shown by the most superficial observation, will consist in a gradual scattered increase of spruce at the expense of the alders, but the manner thereof is not yet entirely clear. The spruces present are contemporaneous with the alders; the shade is at present apparently too dense for further successful germination. A careful search at every opportunity has revealed a few—but very few—seedlings beneath the bushes. Reproduction by layering, a habit to which the spruce is much addicted (Cooper, '23, p. 241; Cooper, in press), may be of some slight importance. In short, the gradual increase of individual spruces until forest is established and thicket eliminated is an unquestioned fact; the manner of it must await further investigation.

E. SUCCESSION AND EROSION

The shores of Glacier Bay are more or less mantled with glacial detritus—morainic materials and their water-borne derivatives. These unconsolidated deposits are found in 2 general situations. The lowlands, mainly surrounding Muir Inlet, bear the "low-level gravels," and the steeper slopes are veneered

with rather amorphous lateral moraine accumulations and the associated "high-level gravels" (Cooper, '23, p. 104). The low-level gravels are of great extent, only a minor portion of them having yet been uncovered. They

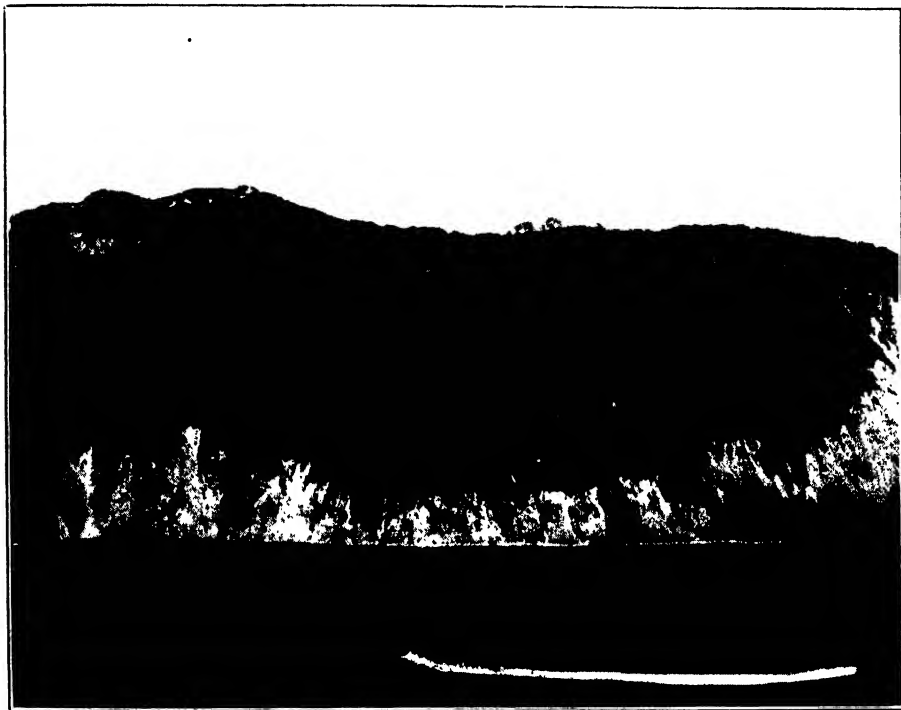


FIG. 11. Mountain slope east of lower bay, near Sandy Cove. Alder thicket with scattered spruces rising above. At the top an area of ancient forest above the limit of the last glacial advance. (Cooper, '23, pp. 123-125.) Photograph by Alaskan Aerial Survey.

are relatively stable except that the margins facing the bay are cliffed and gullied by wave and stream action. Upon their surfaces the succession develops normally, being rarely subject to interruption by erosion. In lower Muir Inlet, where glacial streams have cut canyons, the upper, older surfaces support mature alder thicket and the lower, younger terraces bear scattered alders, with pioneers still persisting.

The high-level deposits are found upon most of the steeper slopes, particularly in the northwest arm. Certain of the fiord-walls, such as those of Johns Hopkins Inlet, are altogether too steep and smooth ever to have retained any, and from some mountain sides they have been completely washed away. Nearly everywhere, however, there are some remnants of gravel and till, and in many parts of the bay we find extensive deposits. Upon these materials, left clinging precariously to steep mountain sides, vegetation must for a long

time maintain an uncertain hold. Multitudes of streams course down the walls, growing to torrents during periods of particularly heavy rains. There is considerable danger in traversing such slopes, for the descent of water, rock and soil sometimes reaches landslide proportions. Once, during a heavy downpour, the grinding roar of sliding and slumping rocks came to me intermittently for half an hour from a single ravine a mile distant. Such slopes rapidly become seamed with steep-sided gullies. The eroded materials are carried down to the bordering flats, if such exist, or are deposited directly in the water. Delta fans are built out into the bay, very large ones occurring at the mouths of valleys where the materials from many gullies are concentrated.



FIG. 12. Mountain slopes near Sandy Cove, lower bay. Alder thicket upon lateral moraine or high-level gravels; gullying still in progress. Photograph by Alaskan Aerial Survey.

At station 26, opposite Russell Island, there is an excellent example, the shore line having been extended a thousand feet between 1916 and 1929.

Successional progress upon the temporarily stable surfaces begins in the normal manner, but these areas are being constantly reduced by gullying. Now begins a contest between erosion and stabilization, the outcome of which differs according to local conditions. A carpet of vegetation greatly hinders removal of soil materials, by making more difficult the enlargement of gullies already formed and preventing the initiation of new ones. The firm-textured

mat of *Dryas*, persistently mantling the eroded slope even when undermined, is particularly effective (Fig. 9). The thicket is even more so because of the deeply penetrating roots; and forest, once established, brings practically complete stability. If, on the other hand, the gravels are completely removed before vegetation can make effective its stabilizing influence, the successional process will be greatly modified both in character and rate; the rock surface succession, with its very deliberate movement, will be substituted for the comparatively rapid progress possible upon unconsolidated materials. Doubtless in some cases the rocks are completely stripped, but many areas, subject to less violent abuse, finally attain stability, the intensity of gullyng gradually decreasing and vegetation covering the whole. On the steep eastern shore of the lower bay there are great expanses of gravel veneer completely grown over—in the vicinity of Sandy Cove with alder thicket and farther south with spruce forest. At certain points there has been little gullyng from the first, for ice-formed contours, notably certain narrow benches, descending southward, stand out plainly in spite of thicket and forest cover. In strong contrast are contiguous areas where gullyng is still extremely active (or possibly rejuvenation may have taken place), even mature alder thicket being undermined (Fig. 12).

F. THE FORELAND EAST OF THE BAY

The foreland east of the lower bay presents certain features of geological and ecological interest not occurring in the bay region proper. Point Gustavus, marking the entrance on the east, is part of the moraine system related to the apparent limit of the recent advance. From this point the moraine swings sharply to the northeast and thus recedes rapidly from the shore of Icy Strait. The ice at its recent maximum thus covered but a minor portion of the foreland, which is in the main a great marginal outwash plain. So far, this region has been touched at but a single point (station 53), but plans for the future include a thorough investigation, in which an airplane survey forms an almost essential part.

The plain slopes very gently southward to Icy Strait, where it is bordered by a tidal flat of great width. The surface is furrowed by shallow abandoned channels, and occasional small streams with tidal estuaries drain the area. A local settler reports the presence in the interior of lakes of considerable size which are very possibly outwash kettles.

The dominant vegetation-type, so far as can be seen from the shore, is youthful spruce forest of the sort occurring along the margins of the lower bay. The southern boundary of this community is irregular, the forest extending out in tongues along the uneroded surfaces between the abandoned channels, and displaying in most places an imperfect bordering zone of pines (*Pinus contorta* Dougl.). The empty channels support a scattered growth of pines and willows, except in the lower spots, which are occupied by a wet meadow community. Between the forest and Icy Strait there is first a broad

expanse covered by a vegetation-type, frequent along the shores of south-eastern Alaska, which may appropriately be termed "beach meadow." The characteristic species are as follows:

- Agropyron violaceum* (Hornem.) Lange.
- Elymus arenarius* L. Beach rye.
- Torresia odorata* (L.) Hitchc.
- Spiranthes romanzoffiana* Cham. Lady's tresses.
- Fragaria chiloensis* (L.) Duch. Beach strawberry.
- Lathyrus maritimus* Bigel. Beach pea.
- Angelica genuflexa* Nutt.
- Dodecatheon pauciflorum* (Durand) Greene. Shooting star.
- Gentiana acuta* Michx.
- Rhinanthus crista-galli* L.
- Achillea borealis* Bong. Arctic yarrow.
- Senecio pauciflorus* var. *fallax* Greenm. Ragwort.

Occasional willows occur, but there is nowhere any suggestion of the typical willow-alder thicket of the bay shores. Pine seedlings are frequent in the upper portion of the meadow. As we pass toward the Strait, the meadow plants one by one disappear, *Elymus* remaining longest. *Plantago maritima* L. (sea plantain) appears and becomes dominant, with it growing *Hordeum boreale* Scribn. and Smith and *Triglochin maritima* L. Where the plant carpet becomes discontinuous *Glaux maritima* L. is found scattered thickly, and last of all the grass, *Puccinellia paupercula* var. *alaskana* (Scribn. and Merr.) Fern. and Weath., makes a broken carpet upon the otherwise bare mud flat.

This description suggests at once a successional series very different from the normal process upon the shores of the bay: a halarch succession correlated with filling-in along the border of the strait. As the submerged soil level in a given spot gradually rises, plants of brackish shores establish themselves, to be superseded by the beach meadow type when the deposit is built up above high tide level. This in turn gives way to forest, the pines preceding the spruces. No thicket stage intervenes, the trees appearing in the meadow very gradually. The reasons for this striking divergence from the process normal in the bay region are yet to be discovered. Physiographic and vegetational processes are now proceeding slowly, but they must have been rapid while streams from the nearby ice front were actively at work.

III. The Interglacial Forest

John Muir and other early visitors observed along the shores of Glacier Bay the remains of an ancient forest, which lived during the interglacial period preceding the most recent advance of the ice. During my 2 earlier visits, and especially in 1921, I made a careful study of these relics (Cooper, '23, pp. 104-125), and in 1929 new materials were discovered which constitute the subject of the present section. As an introduction I will quote briefly from the summary to the earlier paper:

"During the period of contracted ice fields which preceded the last glacial advance (culminating about a century and a half ago) the shores of Glacier Bay were densely forested from the water's edge to timberline (altitude today about 2,500 feet). The trees grew rooted in part in the crevices of the already glaciated rock surfaces, and in part upon alluvial lowlands of gravel and silt.

"Actual evidence shows that this forest covered both shores of the lower bay, both shores of Muir Inlet as far as the present ice cliff of the Muir Glacier, and the shores of the lower portion of the upper bay. Presumably it extended farther in various directions—east and west beneath the stagnant ice masses bounding Muir Inlet, north beyond the Muir ice cliff, and northwestward along the shores of the upper bay.

"In character it was identical with the mature climax of southeastern Alaska today. The tree species were Sitka spruce (*Picea sitchensis*) and hemlock (*Tsuga heterophylla*, or *T. mertensiana*, or both). . . . As in the forest today, mosses made up the bulk of the lower vegetation. . . .

"The forest was destroyed and the remains buried beneath sediments deposited in the course of the last glacial advance. . . .

"The ice in its final retreat has uncovered the gravels, and stream and wave action are continually bringing to light the remnants of the ancient forest."

From one locality (station 15) a wealth of material was obtained which provided a most satisfying picture of the life of the forest floor: 13 species of mosses, plants of *Lycopodium*, fungus mycelium, mycorrhizal rootlets, fragments of the wing of a caddice-fly. No such good fortune rewarded our search in 1929; we did, however, add much to our knowledge of the extent of the forest and its tree composition. Several of the localities of 1921 were given more careful study, two new localities were added in the lower bay (nos. 48 and 49), and, best of all, a group of forest remnants of very special interest was discovered close to the Muir cliff (nos. 45, 46, 47), which in 1921 was buried beneath the ice. Table VII gives the composition of the forest at every station so far discovered, grouped according to 3 general localities.

The most obvious generalization is the large proportion of spruce in Muir Inlet contrasted with great predominance of hemlock in the lower bay. To quote once more:

"It would seem that in the lower bay region, because of the longer duration of the ice-free period, the forest had fully attained the climax state characterized by predominance of hemlock. In the vicinity of Muir Inlet, much nearer to the glacial sources, the period during which forest development was possible was shorter at both ends, and the forest was consequently in the subclimax stage, marked by great importance of spruce."

Since 1921 I have naturally felt much curiosity as to what might be revealed by further recession of the Muir ice front. The findings at station 19, farthest north in 1921, indicated the presence at that point of subclimax forest with considerable hemlock. How great a recession would be necessary to reveal the end of the forest—the line of its farthest interglacial advance? A continuation of the tendency already indicated was to be expected—reduction of the percentage of hemlock and increase of spruce, followed by com-

TABLE VII. *Composition of interglacial forest*

	Sub- stratum	Number of trees sampled	Per- centage of spruce	Per- centage of hemlock	Percent- age of cotton- wood
Lower Bay					
Station 7.....	Silt	1		100	
38.....	Rock	12		100	
49.....	Rock	4	25	75	
48.....	Rock	2		100	
Total.....		19	5.3	94.7	
Lower Muir Inlet					
Station 14.....	Rock	24	46	54	
15.....	Silt	36	81	19	
16.....	Rock	9	45	55	
20 north (lower).....	Silt	15	100		
20 " (upper).....	Gravel	23		17	83
20 south.....	Rock	8	13	87	
17.....	Rock	14	93	7	
18.....	Silt	1		100	
Total.....		130	56.1	29.3	14.6
Upper Muir Inlet					
Station 19.....	Rock	4	50	50	
45.....	Gravel	10	70	30	
46.....	Gravel	20	100		
47.....	Rock	22	27	73	
Total.....		56	62.5	37.5	

plete disappearance of hemlock, and this by replacement of the conifers by thicket or cottonwood forest—in other words, the succession in reverse order.

Between 1921 and 1929 the cliff of the Muir Glacier retreated approximately 2 miles, exposing a considerable extent of gravel flat and glaciated rock surface. Here were found new forest remnants in the 3 places indicated on the sketch map (Fig. 13).

Station 46. A gravel bluff displays an ancient forest level at a height of 48 feet above high tide. The peaty deposit is in several very thin layers much impregnated with silt. Twenty trunks were sampled and every one proved to be a spruce.

Station 47. This is a rock terrace 35 feet above high tide at the south end of the peninsula which projects into the inlet a short distance from the Muir cliff. It was originally covered with mature forest, the roots of the trees being well anchored in the crevices. Large stumps have been ground down by the ice until they are mere rounded protuberances. Other stumps were visible high up on the slopes of the rocky hill to the north. Twenty-two trees were sampled, of which but 6 were spruces and the rest hemlocks. All sizes were included in the count here as in other localities. In order to learn more as to the dynamics of the old forest, 2 restricted areas were selected in which mature trunks and suppressed individuals were considered separately. These, combined, give the figures presented in Table VIII.

TABLE VIII. *Mature and suppressed trees in interglacial forest at station 47*

	Total number of trees	Percentage of spruce	Percentage of hemlock
Mature.....	9	22	78
Suppressed.....	8		100

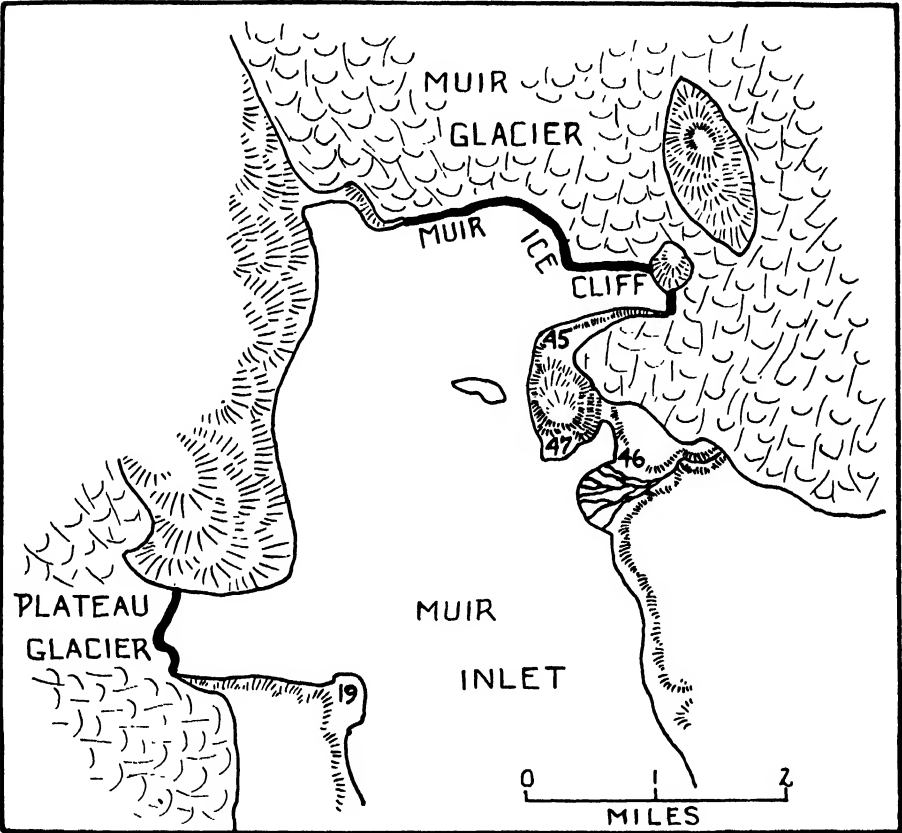


FIG. 13. Sketch map of vicinity of Muir Glacier terminus (1929) showing location of newly exposed areas of interglacial forest.

Such a condition is characteristic of forest in an advanced stage of development. This area, which may fairly be termed mature climax, contrasts sharply with the distinctly subclimax stand at station 46.

Station 45 is on the north side of the promontory of station 47, facing the ice cliff of the Muir Glacier and less than a quarter of a mile from it. The base of the gravel bluff, which is 120 feet high, is almost constantly washed by iceberg waves that are frequently of tremendous size. These maintain the cliff at an angle approaching the vertical, and the narrow berg-strewn beach thus furnishes a rather precarious base of operation.

Two forest levels outcrop in this bluff, the lower 30 feet above the beach, the upper about 40 feet higher (Fig. 14). It was impossible, without undue risk, to obtain specimens from the latter, but the trees rooted in it were evidently smaller and less numerous than those of the lower level, a diameter of 2 feet being the maximum seen. The peat layer at the lower level was thin and flaky. Stumps rooted in it were numerous and large—in diameter up to 3 feet. Ten specimens were obtained, of which 7 were spruces and 3 hemlocks.



FIG. 14. Bluff at station 45, showing stumps of interglacial forest at two levels.
A portion of the Muir Glacier at left.

This group of freshly exposed remnants gives no indication of near approach to the end of the forest. There is, to be sure, the pure spruce stand at station 46, but the effect of this evidence is completely neutralized by the predominance of hemlock at station 47 and its frequency at station 45. We thus find from end to end of the known portion of Muir Inlet areas which had attained to late subclimax or even climax condition at the time of destruction. Station 46, one of the latest to be uncovered, was as mature as any in the lower part of the inlet.

Locally, however, there were great differences in successional status. Inspection of Table VII shows that there is a general correlation between type of forest and substratum. The forests in which hemlocks were abundant (with the unimportant exception of station 18) grew upon rocky slopes or terraces, the trees being rooted mostly in the crevices. In at least 2 such

cases (stations 20 south and 47) there were numerous suppressed individuals, all hemlocks, beneath the dominant stand. The forests of pure or predominantly spruce or cottonwood, on the other hand (with one exception, station 17), grew upon a surface of gravel or silt. In other words, the rocky slopes were covered with forest that had reached almost complete maturity, developed through the centuries of the interglacial period by way of the exceedingly slow rock surface succession; the far less stable alluvial deposits of the period supported communities much younger developmentally.

Extensive alluvial flats of contemporary age do not occur at Glacier Bay, so it is necessary to appeal to other regions for illustration of what happened here in past centuries. The Stikine River, in Alaska and British Columbia, offers unusual opportunities for the observation of the floodplain succession. Upon sand bars and gravel flats the first dominants are western cottonwoods (*Populus trichocarpa* T. and G.), which rapidly form a pure forest. Beneath these an alder thicket develops; the aging cottonwoods drop out one by one and the alders are left in control; Sitka spruces gradually appear and finally supersede the alders, and the addition of the hemlocks completes the process.

The extensive lowlands around Muir Inlet, now mainly ice-covered, but exposed during the interglacial period, must have provided abundant opportunities for successional series of this type. Especially during the glacial advance which followed, characterized as it was by the laying down of stratum upon stratum of gravel, sand and silt, vegetational development must have begun again and again. Usually it was arrested in the earliest stages, but occasionally considerable advancement was attained. The upper forest level at station 20 north, described in my earlier paper (Cooper, '23, pp. 119-122), and given additional study in 1929, is a case in point. We have here the relics of a community in transition from cottonwood forest to alder thicket. Twenty-three stumps were identified, of which 19 were cottonwoods and 4 hemlocks. In the scanty peat layer were found cottonwood buds and bud-scales, fruiting alder catkins, infrequent mosses and mycorrhizal rootlets. The early arrival of hemlock, with no spruces so far as the evidence goes, is unusual but by no means unknown. A later phase of the floodplain succession is seen at stations 20 north (lower) and 46—pure spruce forest with neither cottonwood nor alder. Still more advanced are stations 15 and 45, where hemlocks had made their appearance in small numbers.

In this connection an interesting question suggests itself, which must await further evidence for solution. The existence of superposed forest levels at 2 points separated by a distance of 7 miles may possibly indicate a general halt in the advance of the ice or a temporary recession, during which building up of the gravels ceased for a time sufficient to permit development of forest upon the alluvial surfaces. It is just as possible, on the other hand, that there is no common causal relation between the 2 forests, each being due to a local deflection of the sediment-bearing streams.

PHYSICAL CONDITIONS IN SUN AND SHADE

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INTRODUCTION

Students of the relation of environmental conditions to the distribution of organisms have long recognized the fact that relatively great differences in conditions may occur within areas of very restricted size. Certain environmental conditions are more constant from spot to spot than are others; but the entire complex upon which the life and distribution of the organism depends, is to be thought of as uniform only throughout areas or volumes of extremely limited dimensions. It follows that the customary manner of measuring climatic conditions, so well suited to the purely physical requirements of meteorology, can give the student of environment nothing more than a normal base from which to determine the departures in the various habitats of an area.

Physiological work has given us a large body of facts relative to the influence which difference intensities of a given condition are found to exert on various physiological processes. Very few of these relationships can be expressed by straight line curves. Not only may a small difference between 2 environments be of importance, but the same number of units of difference may vary in effect at different intensities of the condition under investigation. The importance of a given degree of difference can be ascertained only by determining its influence upon some specific life process. The study of environmental conditions can be fruitful for biological purposes only when it is carried on in close conjunction with the investigation of the physiology of the organisms which live under that environment. An important part of the program of the Desert Laboratory comprises such a study of the physiological behavior of a small group of plants, together with the intensive study of the conditions in their natural habitats. Some of the larger habitat differences in the vicinity of the Desert Laboratory have been determined in the work of past years. Further work is being directed to determining the conditions for a number of localities in which differences in the dominant vegetation, or in the seasonal behavior of the vegetation, would seem to indicate that differences in the environment are operative on a small scale.

INFLUENCE OF SHADE IN ARID REGIONS

Throughout the arid parts of the United States and Mexico it may be commonly noted that the shade of the large bushes and desert trees supports a much larger number of herbaceous plants, root perennials and seedling per-

ennials than do the unshaded areas alongside them. In southern Arizona not only are the herbaceous annuals more abundant in the shade of the small trees, especially in the summer rainy season, but they reach greater size there than elsewhere and continue their vegetative activity longer than they do in the open. The shade is no more favorable than the open for the germination of the seeds of the larger perennials, but it is far more favorable for these plants during the very critical rainless periods in their early history. The survival of many of the young perennials which spring up in the shade of *Parkinsonia*, *Olneya*, *Prosopis*, or other trees, leads to a grouping of the perennials, which is a conspicuous feature of the vegetation. It is often asked why *Parkinsonia* and *Carnegia* so frequently grow in close juxtaposition. In all such cases the *Parkinsonia* is older than the *Carnegia*, and the latter has secured its start through the better conditions in the shade of *Parkinsonia*, as well as through the protection from mechanical injury which the tree afforded.

It is obvious that the larger trees and shrubs, already well established, serve to provide small areas in which the conditions are more favorable than they are in the openings which separate the large perennials in the widely spaced vegetation of the desert. It seems probable that the ameliorating influence of the shade affects nearly all of the environmental conditions at least slightly. The results of this are most conspicuous during the weeks following the rainy periods, and it seems probable that there is then a greater difference between shade and sun conditions than there is in the midst of long dry periods. The effect of shade in merely prolonging the favorable conditions, and reciprocally shortening the duration of the adverse ones, is in itself of great importance to the seedlings of perennials.

STATIONS FOR MEASUREMENT OF SHADE AND OPEN CONDITIONS

During the growing season of 1929 an investigation was made of the difference between certain conditions as measured in the open and under the shade of a palo verde tree (*Parkinsonia microphylla*). My thanks are due to Mr. T. D. Mallery for valuable aid in connection with this work. The stations for measurement of shade and open conditions were located 7 meters apart on a nearly level outwash slope, or bajada, on the grounds of the Desert Laboratory. The soil is coarse rhyolitic outwash, with a surface covering of angular stones, and a subsoil of heavy basaltic clay. The subsoil is outwash from the basaltic Tumamoc Hill, east of the stations, while the rhyolitic surface soil is derived from the foothills of the Tucson Mountains to the west. The tree under which the shade conditions were determined has a height of 4.3 m., a spread of 6.8 by 5.7 m. and a trunk circumference of 1 m. The branches of the tree hang low, within 1.0 to 1.4 m. of the ground, and the shade which it casts is a light one, continuous for only a few patches of shade thrown around the periphery of the shadow of the tree in the early morning and late afternoon. The leaves of *Parkinsonia*, which appear in the rainy

seasons and persist for 2 to 6 weeks after their close, are so small as to make little difference in the shade cast by the tree.

METHODS OF MEASURING AIR AND SOIL TEMPERATURE, EVAPORATION, SOIL MOISTURE AND PRECIPITATION

Measurements of air temperature were made only under the tree, as previous determinations have shown that there is no difference between the readings of properly protected thermometers under these and similar conditions. Weekly readings of absolute maximum and minimum were made. Records of soil temperature were secured with Friez soil thermographs at depths of 7.5 cm. (3 in.) and 30.5 cm. (12 in.) in open and shade. These instruments were calibrated before and after installation, were checked during the season by inserting soil thermometers alongside the bulbs, and were again calibrated on removal. Measurements of evaporation were made with Livingston spherical atmometers in open and shade, to the readings of which the customary corrections were applied. The instruments were exposed with the bulbs 30 cm. above the surface of the ground. Weekly determinations of soil moisture were made in open and shade at a depth of 15 cm. Samples were dried to constant weight in a Freas oven and percentages of moisture were determined on the basis of dry weight. The precipitation data given were secured at the Desert Laboratory, 1,300 m. distant, the total being checked against the seasonal total for a volumetric field rain gage installed near the tree.

TEMPERATURE OF AIR AND SOIL

The seasonal course of the air temperature is shown in figures 1 and 3 in the form of weekly readings of absolute maximum and minimum. The lowest maximum was 69° F.¹ in February, the highest 115° in June; the lowest minimum was 27° in February, the highest was 74° in July.

The data for the temperature of the soil are given in the graphs in figures 1, 2, 3, and 4, together with the concurrent air temperatures. Each of the graphs is drawn so as to show the difference between the conditions in sun and shade at the given depth. The greatest contrast between the soil temperature in the open and under the *Parkinsonia* tree is found in the weekly absolute maxima for the 7.5 cm. depth (Fig. 1). During February and March the air maxima were higher than those of the soil, but with the advance of spring the soil maxima became greater and remained so until November. Twice during the summer the soil maximum in the open was 14° higher than the air maximum for the same week, although the highest soil maximum for the year, 124°, was only 9° higher than the air maximum for the same week. From the middle of March to the middle of May the soil temperature climbed very rapidly from 75° to 109°, and during October and November there was an equally rapid fall from 106° to 80°. Both air and soil temperatures

¹ All temperatures are given in degrees Fahrenheit.

reached their maxima in the arid fore-summer, and then fell and rose irregularly during the summer rainy period of July, August and September. The soil temperature at 7.5 cm. in the shade of *Parkinsonia* followed a seasonal course very much like that of the temperature at the same depth in the open, but from 11° to 25° lower, and consistently below the maxima for the air. The lowest maximum at 7.5 cm. in the shade was 56° in the week of March 18. The maximum for the same week in the open was 75° . The absolute

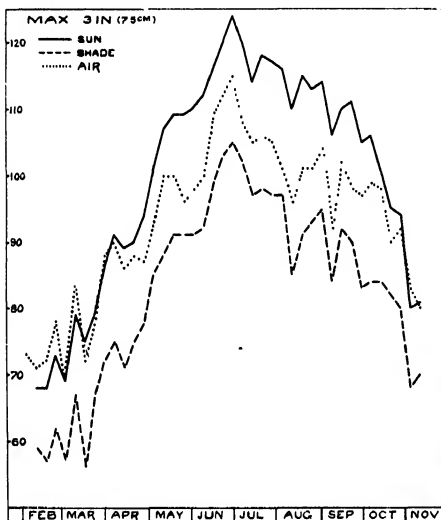


FIG. 1. Weekly maximum soil temperature in sun and shade at depth of 3 in. (7.5 cm.), and weekly maximum air temperature.

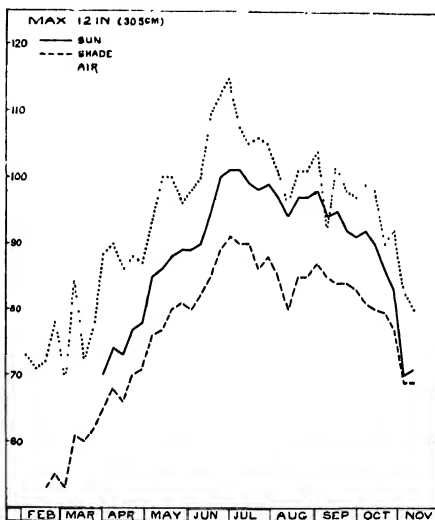


FIG. 2. Weekly maximum soil temperature in sun and shade at depth of 12 in. (30.5 cm.), and weekly maximum air temperature.

annual maximum was 105° in the shade and 124° in the sun on the same week. The several marked depressions of temperature during July, August and September were due to heavy rains, and it is to be noted that the difference between sun and shade temperatures is usually greater during one of these depressions than before.

The course of the weekly maximum sun and shade temperatures of the soil at a depth of 30.5 cm. is shown in figure 2. With a single exception the soil readings are all lower than the simultaneous air maxima. The annual maximum at 30.5 cm. in the open was 101° , or 23° lower than the maximum at 7.5 cm. registered in the same week ending July 1. The march of the soil temperature is more conservative at 30.5 cm. than at 7.5 cm., as always, and the greatest differences between soil and air maxima are therefore at the time of sharp rises in the air temperature. In such cases the soil in the open at 30.5 cm. was from 14° to 16° cooler than the air, at the time of the daily maximum. It will be noted in figure 2 that the soil maxima in the open run

closer to the air maxima in the rainy months, July, August and September than they do in the dry months, April, May and June.

In figure 3 are shown the weekly absolute minima for open and shade at the 7.5 cm. depth, together with the air minima. With only 2 exceptions, all of the soil minima are higher than those of the air. There is much less difference between the temperatures in shade and open in the case of the minima than in the case of the maxima. During the dry months, April, May and June, there was a very close correspondence between the minima in shade and

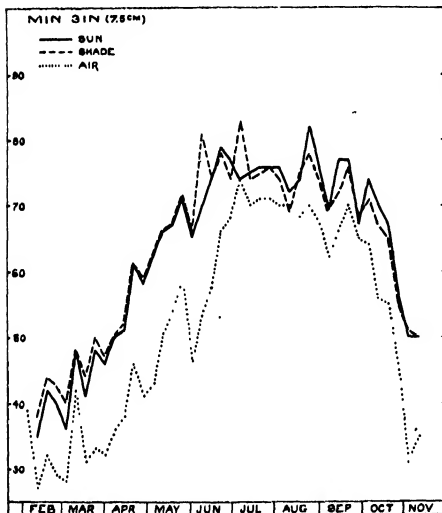


FIG. 3. Weekly minimum soil temperature in sun and shade at depth of 3 in. (7.5 cm.), and weekly minimum air temperature.

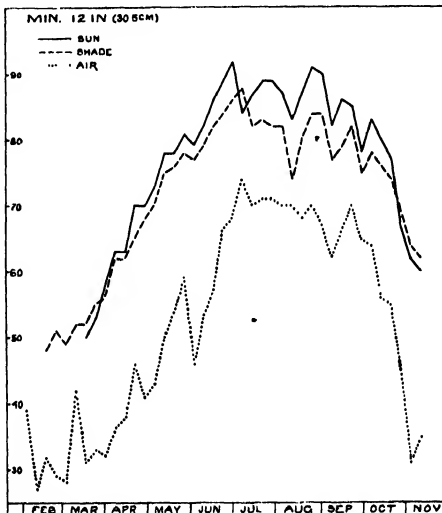


FIG. 4. Weekly minimum soil temperature in sun and shade at depth of 12 in. (30.5 cm.), and weekly minimum air temperature.

open, with the shade slightly warmer. During the 3 wet months following, the relation between the two is irregular, minima in the shade being higher than in the open.

The graphs for the absolute weekly minimum temperature at the 30.5 cm. depth are shown in figure 4. The soil minima are, in general from 10° to 25° higher than those of the air. The minimum at 30.5 cm. is almost constantly lower in the shade than in the open. On passing from the dry to the rainy months the difference between shade and open tends to increase, and the difference between air and soil tends to decrease. It is noteworthy that in the 2 weeks of February and March on which the air minimum fell below 30° the soil minimum at 30.5 cm. was 51° and 49° respectively.

The character of the weekly graphs of soil temperature is shown in figure 5, which is drawn from the original record slips for the week ending June 28. The upper graphs show the temperature at 7.5 cm. in the open (solid line) and shade (broken line). There is a close agreement between the minima

and a difference of 16° to 20° in the maxima. Also there is a lag in the shade maximum which brings it about 2 hours after the maximum in the open. The lower graphs indicate the temperatures at 30.5 cm. in the open (solid line) and the shade (broken line). As compared with the curves for 7.5 cm. they are smoothed to a much smaller amplitude, with the consequent separation of the sun and shade curves, even at the minimal points. The 30.5 cm. curves are slightly lower than smoothed forms of the 7.5 cm. curves would be, and there

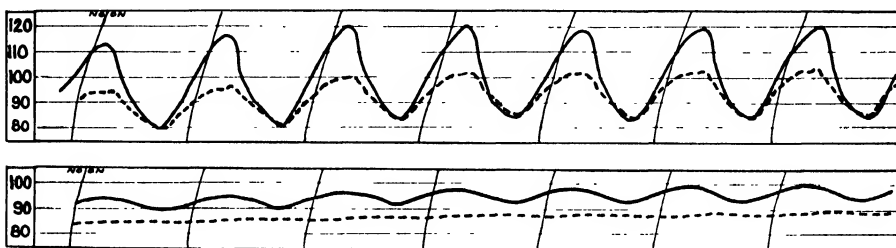


FIG. 5. Graphs showing course of soil temperatures for week ending June 28, 1929. Upper diagram at 3 in. (7.5 cm.), lower at 12 in. (30.5 cm.). Graphs for soil exposed to sun, solid lines; for soil in shade, broken lines.

is a greater lag in the maxima, especially in the shade, where the weakly indicated maximum does not occur until midnight or slightly later.

The opening of the summer rainy season usually takes place in the first week in July, and is responsible for a rapid and profound change in all of the environmental conditions. The data shown in Table I have been worked out in order to determine whether the differentiation between the soil temperature conditions in shade and sun is greater in the 2 driest months of the growing season or in the 2 wettest. The figures given are the averages of the weekly extremes for the months indicated. There appears to be a slightly greater contrast between shade and open in the humid months than in the dry ones.

TABLE I. *Differences between soil temperatures in shade and open at 7.5 cm. (3 in.) and 30.5 cm. (12 in.) in May and June (dry) and July and August (rainy)*

Datum	Depth	Dry months	Rainy months
Maximum	3 in.	18.0	20.2
Maximum	12 in.	9.0	11.5
Minimum	3 in.	1.4	1.6
Minimum	12 in.	3.1	5.4

The relation between the temperature of the air and that of the soil is a complicated one. Since the temperature of the air is so largely determined by that of the soil, much importance attaches to the percentage of sunshine, the intensity of radiation, the color, character of surface and vegetative cover of the soil. The daily march of soil temperature at a given depth, and the gradients of change in temperature at successive depths, are dependent on the spe-

cific heat of the soil, and the relation of its moisture content to its specific heat and to its agency in the conduction and radiation of heat. In Table II are contrasted the departures of the soil temperature in the open from the temperature of the air for the two driest and the 2 wettest months of the year. The advent of the rainy period increases the departure of the maximum soil temperature at 7.5 cm. and decreases the departure in the other data given.

TABLE II. *Departures of soil temperature in the open from temperature of the air, for May and June (dry) and for July and August (rainy)*

Datum	Depth	Dry months	Rainy months
Maximum.....	7.5 cm. (3 in.)	+ 8.2	+12.1
Maximum.....	30.5 cm. (12 in.)	-12.1	- 6.1
Minimum.....	7.5 cm. (3 in.)	+15.7	+ 6.7
Minimum.....	30.5 cm. (12 in.)	+27.2	+17.5

SOIL MOISTURE

The seasonal course of the soil moisture at a depth of 15 cm. is shown in figure 6. During February, March and April the moisture content was fluctuating, in response to the rains which fell at intervals of from 1 to 3 weeks. Three of the 6 determinations show a lower moisture content in the shade than in the open, which cannot be satisfactorily explained on the basis of the precipitation being greater in the open. On March 11 the soil samples were taken a few hours after a rain of .22 inch and showed a moisture content of 14.5 per cent in the shade and 7.6 per cent in the open. During the succeeding fortnight there was no precipitation, and the moisture content of the soil on March 25 was 7.4 per cent in the shade and 10.0 per cent in the open. The same relation existed on April 1, but was again reversed on April 15, possibly as a result of the rain of .24 inch on April 4. The drain made upon the soil moisture by the herbaceous plants growing in the shade of the tree is an unmeasured factor of importance in this connection. After the death of these plants and the arrival of dry conditions in the latter part of April, the soil moisture in the shade remained consistently higher than in the open throughout the remainder of the growing season. The numerous rains which fell between July 8 and August 19 did little to bring about the difference between the moisture in shade and open which might be expected, undoubtedly because of the high percentage of cloudiness during these weeks. The heavy rain of 2.99 inches on September 24 resulted in a marked increase of the soil moisture in the shade at the next fortnightly reading on September 30, but during the 6 days intervening there had been time for the moisture in the open to fall to the same amount determined before the rain.

In the open the soil moisture content runs a more uniform course than in the shade, and shows a relatively small difference in the dry and wet months. The soil involved is a fine clay, highly retentive of its moisture, having a mois-

ture equivalent of 30. The precise relation of the incidence and amount of rainfall to the fluctuations in the moisture of the soil is complicated by a number of considerations which have been only partially investigated.

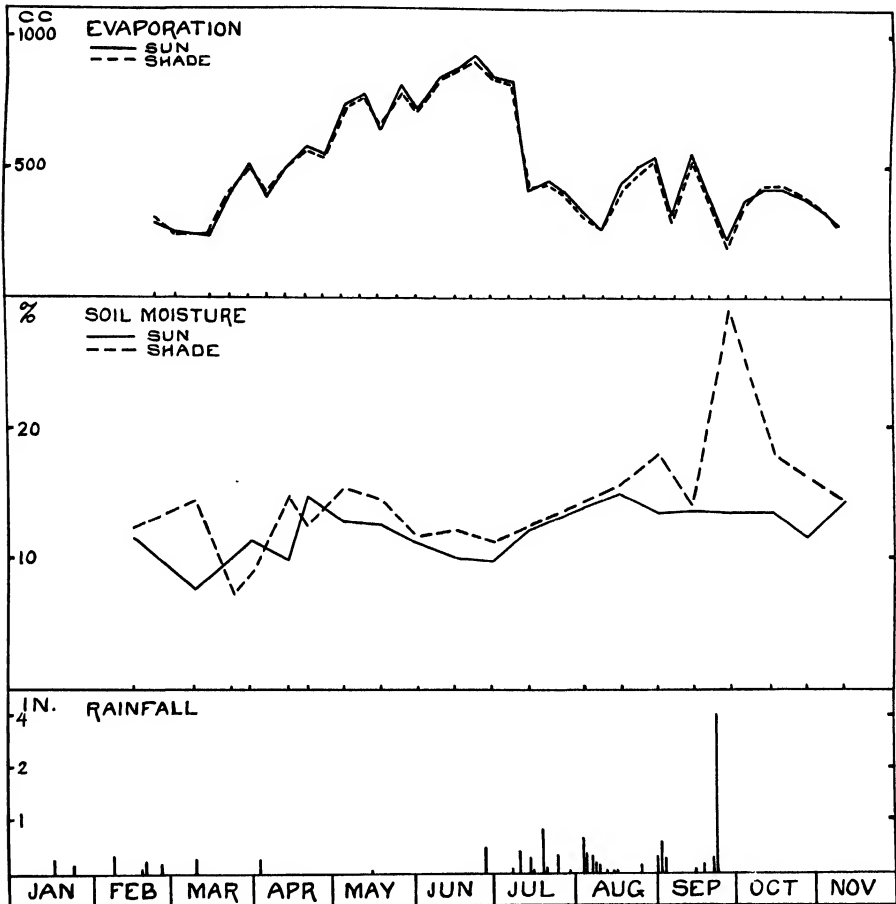


FIG. 6. Graphs showing weekly course of evaporation in sun and shade, and of soil moisture at 15 cm. in sun and shade, together with diagram showing incidence of rainfall.

EVAPORATION

The march of evaporation in sun and shade is shown in figure 6. Readings were taken weekly and are given in cubic centimeters of loss per week from a standard spherical atmometer cup. There was an irregular but continuous rise in evaporation during the dry period from the middle of March to the end of the first week in July. The fluctuations during this period are due to variations in temperature and wind movement. The opening of the rainy season was accompanied by a sharp fall in evaporation from 823 cc. on the week ending July 8 to 403 cc. on the week ending July 15. The fluctua-

tions in rate during July, August and September were due to the incidence of the rains, with their accompanying cloudiness and high humidity.

Throughout the season there was a tendency for the evaporation in the shade to be slightly lower than that in the sun, although there were 10 weeks in which it was slightly higher. The close coincidence between the evaporation rate in sun and shade indicates that the humidity, air temperature and air movement, all so nearly alike in sun and shade, are too important in controlling evaporation to be outweighed by the difference in radiant energy in full sunlight and in the light shade of *Parkinsonia*. The close agreement between readings of evaporation from the atmometer in sun and shade is only indirectly related to the relative water loss of plants in sun and shade.

SUMMARY

Under desert conditions the light shade of a tree or large bush supports a heavier stand of herbaceous annuals and seedling perennials than will be found in the open. A comparison of evaporation, soil moisture and soil temperature at two depths has been made in the open and in the shade of *Parkinsonia* on the grounds of the Desert Laboratory, at Tucson, Arizona. The weekly totals of evaporation are very nearly the same in shade and open throughout the growing season. The moisture of the soil at 15 cm. is usually greater in the shade, but the difference between sun and shade readings is of significant magnitude only after very heavy summer rains or lighter rains in the cooler months. The soil temperatures in sun and shade exhibit important differences, both at 7.5 cm. (3 in.) and 30.5 cm. (12 in.), particularly with reference to the maxima. At 7.5 cm. the absolute annual maximum was 105° in the shade, and 124° in the sun, while the absolute air maximum was 115°. During the four mid-summer months the average difference between the maximum soil temperature in sun and shade was 19.1° at 7.5 cm. and 10.2° at 30.5 cm. During the same period the average difference between the minima was 1.5° at 7.5 cm. and 4.2° at 30.5 cm. The annual absolute minimum air temperature was 27°, and in the same week the absolute minimum soil temperature was 35° in the open and 38° in the shade.

The relatively close correspondence between evaporation and soil moisture in sun and shade indicates that the vegetational differences between these habitats are perhaps not greatly dependent upon differences in moisture conditions. The differences in solar radiation in the two habitats are not only responsible for the important differences in soil temperature conditions, but also for differences in the water loss of plants, which are known to be inadequately indicated by atmometer readings of evaporation. The intricate interrelationship of moisture and temperature conditions is also concerned in the fact that the deeper roots of plants are warmest at the same time of day that their branches and leaves are coolest, which must serve materially to aid the restoration of moisture content which the plant undergoes at night. Another important aspect of the soil temperature in determining habitat differences is concerned with the optimum temperature for germination of seeds.

STUDIES IN THE VEGETATION OF SOUTHWESTERN TEXAS

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INTRODUCTION

The Grassland Formation of North America for many years has been a center for ecological study. Numerous extensive and intensive investigations have been made, but the area is so vast that for some sections there is even no reconnaissance work. The present investigation deals with the grasslands of southwestern Texas, especially in their relation to grazing. A study has been made of the structure of the vegetation. The recovery of the vegetation from the harmful effects of overgrazing has been investigated by means of chart and clipped quadrats both inside and outside of exclosures. A portion of the Trans-Pecos region, just north of the Rio Grande, and centering about



FIG. 1. A flat valley between low mountain ranges. The cover of grama-grass (*Bouteloua gracilis*) is much overgrazed because of its proximity to a water hole. The slopes are covered with an open growth of cedar (*Juniperus monosperma*) and oak (*Quercus grisea*).

Alpine, 225 miles southeast of El Paso and 100 miles north of the Mexican border is the area studied. This area is but little known geologically, geographically, and botanically (Bowman, '11; Bray, '01, '05). Bray ('06) in his "Distribution and Adaptation of the Vegetation of Texas" discusses it



FIG. 2. General view of rolling topography with mountains in the background. The grama grasses on the left of the fence have been only lightly grazed and flower stalks are abundant.

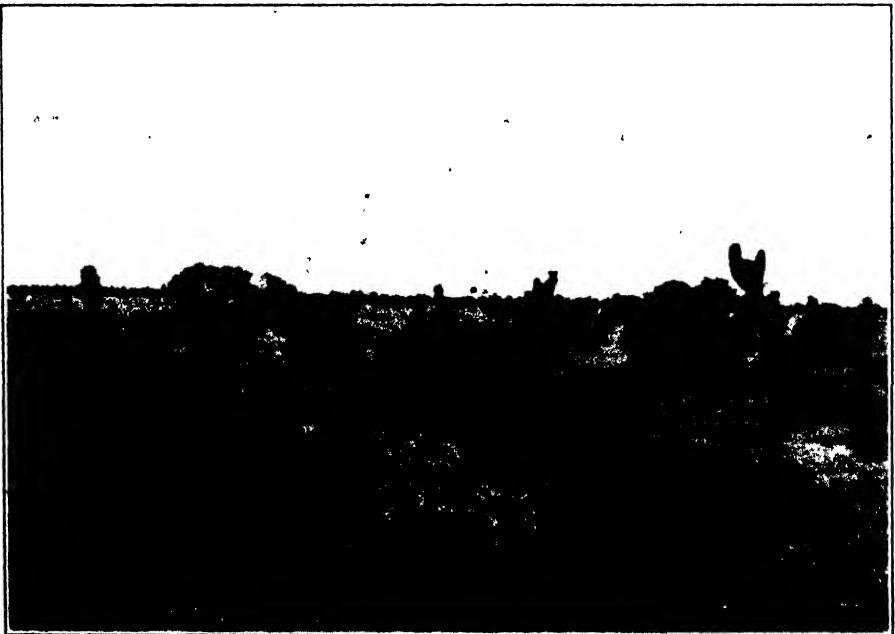


FIG. 3. Representative area of grama grass on Mitchell flat showing the abundance of *Yucca*, *Koeleria*, and *Opuntia*.

only in a general way, and the recent work of Tharp ('26) is confined to the vegetation of Texas east of the 98th meridian. The area is greatly diversified and affords a rich and virgin field for ecological study. It is probably the

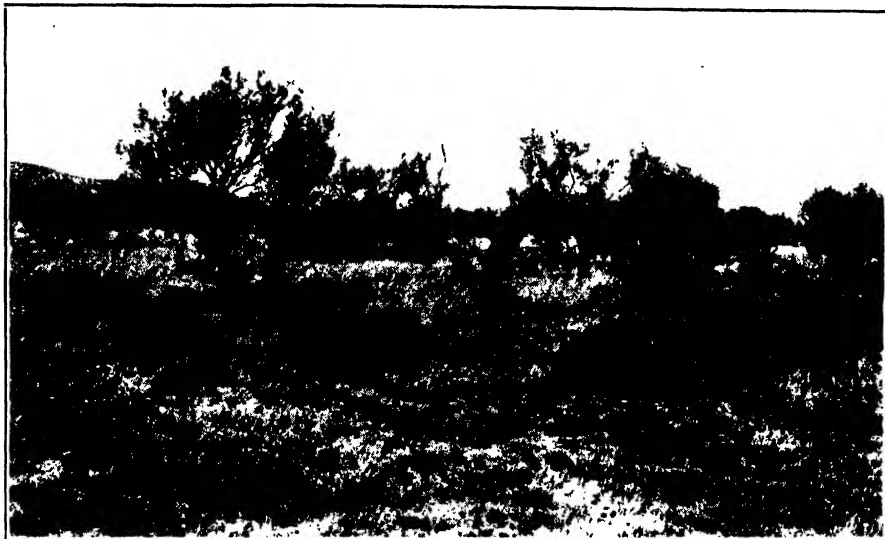


FIG. 4. A society of cat's claw (*Acacia* sp.) on a flat at the Mitchell station. *Bouteloua gracilis* is dominant and well developed.

largest remaining area of native grassland in the United States. It has been continuously grazed since the bison were displaced by white men's herds of cattle (Havard, '85; Smith, '99).

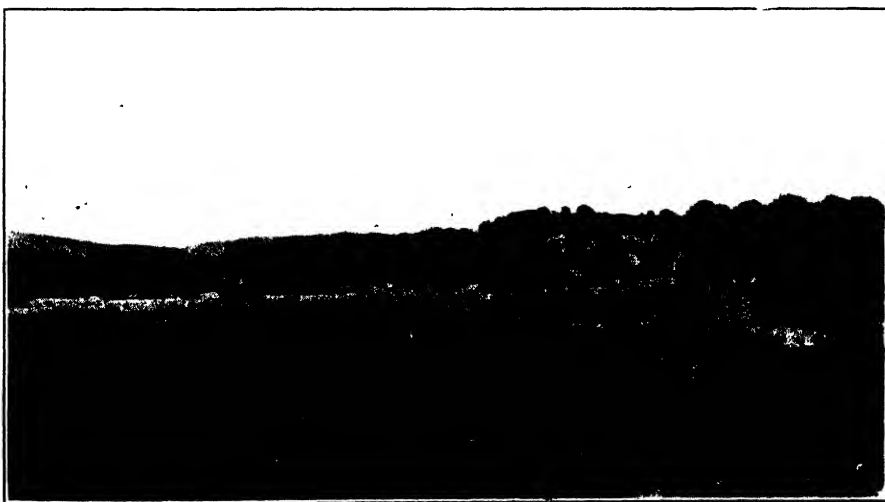


FIG. 5. Red cedar (*Juniperus monosperma*) in the grama-grass sod on thin soil of uplands at the McIntyre station. Note the eroded area in the foreground.

The land is one of high mesas or flats and of broad valleys bordered by outlying buttes and mountains (Figs. 1 and 2). Although the annual rainfall is only about 14.5 inches, the relatively high altitude favorably modifies the high temperature and evaporation of this latitude. This, combined with a soil of good water retaining power, greatly increases the efficiency of the precipitation and permits the development of a short-grass type of vegetation. As a result of continuous grazing in summer and winter, however, the short grasses are now reduced to a very open cover. On the rougher lands and on porous soils, where grazing injury has been especially severe, other xeric types of vegetation occur. Among these are piñon-juniper woodland, yucca, mes-

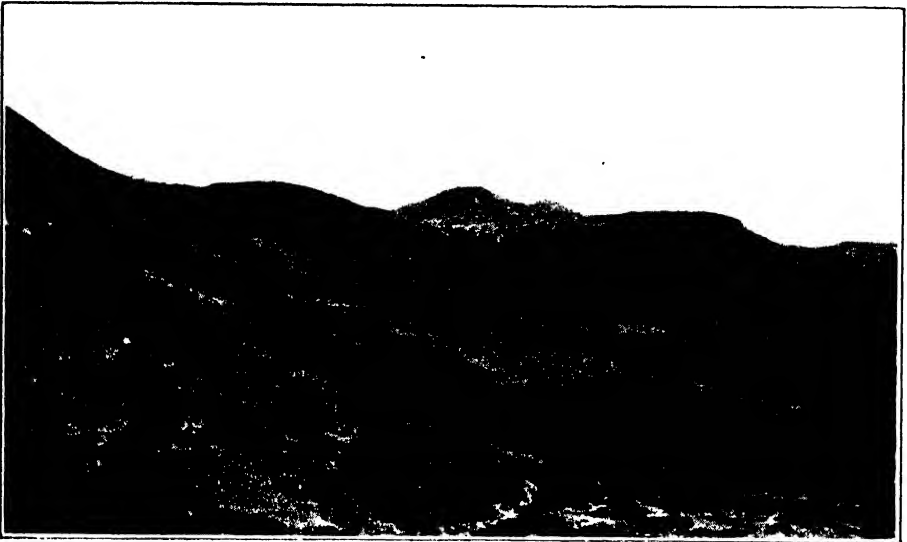


FIG. 6. An open postclimax woodland, mostly *Quercus grisea*, distributed along drainage courses.

quite, and various other desert shrubs. The broken grass cover affords an excellent opportunity for these greatly to increase their territory (Figs. 3, 4, and 5). Along drainage courses where more water is available, narrow bands of postclimax woodland contrast strikingly with the surrounding grassland and desert types (Fig. 6). Oaks, ash, and walnut are among the chief woody species. On intermediate areas the shrubby vegetation (*Prosopis*, etc.) is more mesic than is the desert scrub of the uplands.

Residence in Alpine, in connection with botanical work at the Sul Ross State Teachers College, during 1926-1929, gave excellent opportunity to engage in field work.

LOCATION AND EXTENT OF THE AREA

The area lies between the Guadalupe Mountains on the northeast and the Rio Grande on the southwest in that portion of the Trans-Pecos country locally known as the Big Bend Region. Latitude 30° N. and longitude 104°

W. approximately pass through the center of the region. Altitudinally the area varies from a height of about 4,000 feet on the flats which lie between the more or less detached ranges of buttes and mountains, to about 7,000 feet on the general mountain mass.

An area of 900 square miles lying in Brewster and Presidio counties was most intensively studied, but extensive reconnaissance was made into adjoining areas. As a result of this survey it clearly seems that much of the surrounding territory, including perhaps 10,000 square miles, has a cover of vegetation which, in general, is very similar to that about Alpine.

TOPOGRAPHY

The whole region during the Tertiary age consisted of a high mesa or series of mesas. Throughout long periods of time erosion has molded the surface so that in general two types of topography prevail. One consists of level flats, often many miles in extent, lying between detached mountain chains and isolated mountain masses, and the other of the mountains proper which are the hard cores of the former mesas that more successfully resisted the forces of erosion (Hill, '00). In some cases the original mesas have not

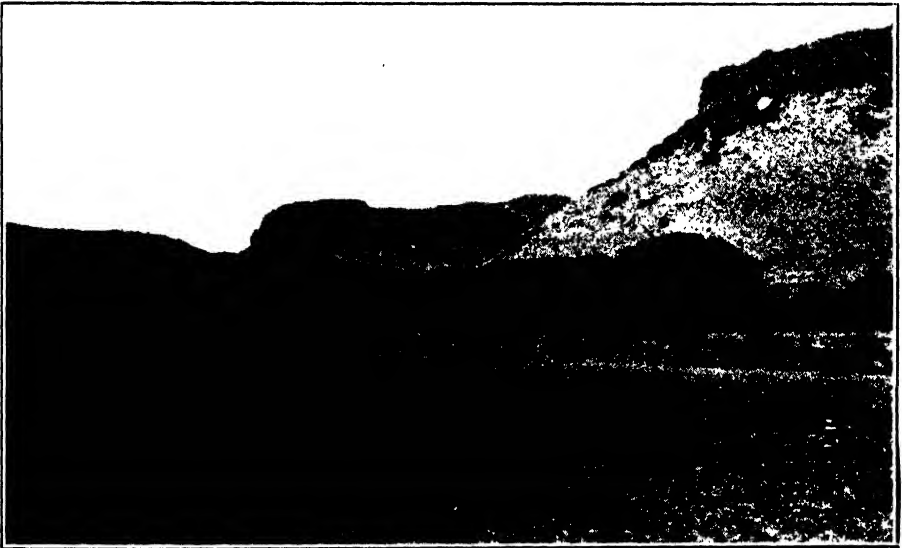


FIG. 7. Flat-topped mountain with vertical walls of igneous rock and steep talus slopes bordering an extensive flat on the Kokernott ranch. Walnut (*Juglans rupestris*) borders the water course which is usually dry.

been entirely removed, and limited areas, sometimes a few square miles in extent, are found above the eroded mountain sides, i.e., above the so-called rim rock (Fig. 7).

The flats or plains between the mountains appear to have been degradation

plains which have later been built up by the outwash from the surrounding mountains. Soil profiles reveal rounded, water-worn boulders at great depths (15-20 feet) with gradual diminution of size of rocks as the surface soil is approached. The surface 1 to 3 feet is often free from rock and consists of well formed soil with a protecting cover of grasses (Fig. 8). Where this cover has been greatly broken by continued overgrazing and trampling, degradation has again begun. In many places arroyos cut deeply and spread widely through the land, the slope being sufficient to afford great momentum to the onrushing water resulting from torrential rains.

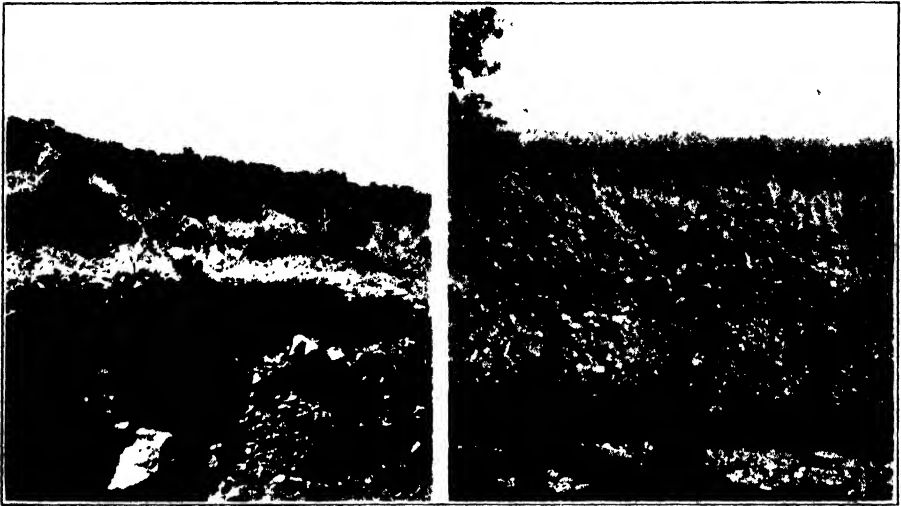


FIG. 8. Soil profiles from the vertical sides of arroyos showing water-worn boulders overlaid by two or three feet of silt-loam soil intermixed with gravel. The one on the right is from Kokernott Springs station.

The mountains lack continuity and exhibit many irregularities and eccentric forms of relief. They often extend two or three thousand feet above the valley flats, and heights of 6,000 to 7,000 feet are frequently attained. The Davis Mountains in the vicinity of Alpine, for example, consist of an extensive group of igneous rocks with the mesas of adjacent, dissected, volcanic plateaus.

In general, the individual mountains present sharp and rugged outlines. The highest are largely conical peaks rising to an altitude of over 8,000 feet. The mountainous part of the region is very rugged, and the slopes are usually steep. Most of the mountains are flat topped, and the igneous walls of rim rock are frequently exposed in vertical cliffs 100 to 300 feet high. At the bases of these occur extensive talus slopes. Many consist of large boulders, but all gradations occur, some having a coarse soil (Fig. 7). The slope from the foot of the cliff to the valley proper is usually one-half to one mile in length. Water from torrential rains has assorted the materials in such a

manner that while the heavier, coarser detritus has been deposited near the mountains, the finest material has been carried to the foot of the slope or on to the mesa itself.

SOILS

In a region of such diversified topography many soil types are encountered. Until extensive surveys are completed no detailed statements can be made. Soils of certain flats consist of clay loam to a depth of 18 inches and are underlaid with a calcareous soil, nearly half of which is calcium carbonate. This is powdery dry and several feet thick.

Quite in contrast are the soils of other apparently similar flats where adobe is found. These may consist of one-third clay and only slightly less silt, with a similar high content of very fine sand. This grayish colored soil may continue rather uniformly to a depth of several feet.

On more rolling flats, the soil is often fairly uniform to a depth of 2 to 4 feet. Although half of the substratum may consist of coarse gravel, a third of the soil is often very fine sand and enough finer soil particles occur to hold the water in the first 2 or 3 feet.

In depressions such as ancient lake beds, a very heavy type of soil is found. It frequently contains more than 50 per cent of clay and although very plastic when wet it is so hard when dry that it can scarcely be removed with a pick. Particles larger than very fine sand make up less than 10 per cent. At a depth of about 3 feet a very calcareous, yellowish subsoil is found.

Soils on the slopes at the foot of the mountains are coarser in texture and show extreme variations. Boulders and coarse gravel may be overlaid with a thin veneer of a fairly well disintegrated rock, but as the mountains are approached surface rocks and boulders become more and more abundant and the soil coarser. Often rock fields support only a vegetation of lichens.

DRAINAGE

The annual rainfall is so low and the climate so arid that the drainage system is immature and no rivers are found. Because of the rugged, mountainous topography, a local torrential rain may result in such a rush of water from the mountain slopes that floods occur several miles away. The rise of water is rapid, drainage channels overflow, and enormous loads of sand and silt are carried by the flood. Arroyos, often having their beginnings in cattle paths or other slight depressions, are the chief lines of drainage, although the rushing waters also cause extensive sheet erosion on the flats. The drainage channels quickly cut through the compact soil, and, once the gravelly and rocky subsoil is reached, the arroyos are widened with alarming rapidity (Fig. 9). But the recession of the flood is almost as sudden as its rise, the water sinking away into the dry soil. Some drainage from mountains to flats also occurs in the coarser subsoil and results in occasional, never failing springs. One of these (Kokernott Springs) has been known since the time of the Spanish

explorers in the sixteenth century. Below the spring is an arroyo over 20 feet in depth and more than a mile in length. The factor of drainage has a marked effect upon the distribution of the water. It is scarcely less important than that of soil type in determining the distribution of the various plant communities.

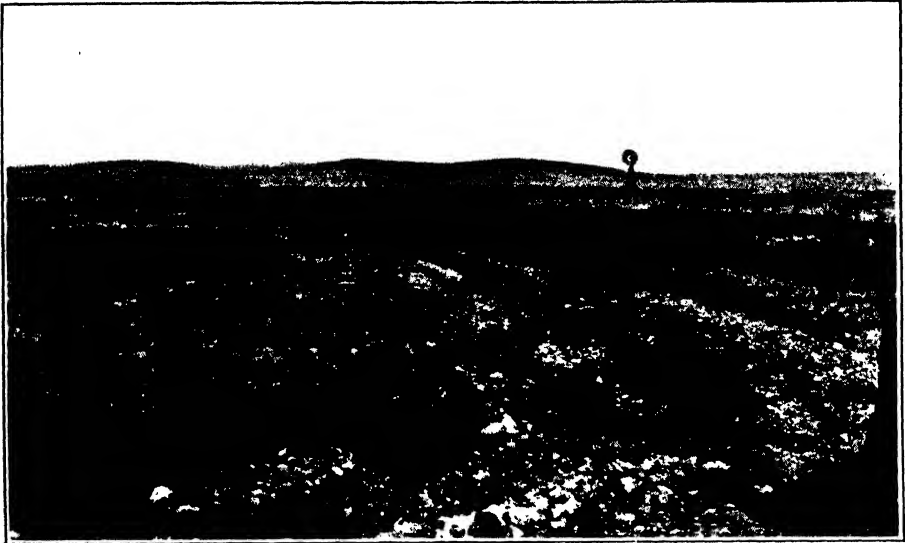


FIG. 9. General view of damage done to range lands by erosion. This arroyo increased in width from 25 to 200 feet in a period of four years.

GENERAL PLANT-LIFE CONDITIONS

Water is the major limiting factor to plant growth, consequently the amount and distribution of the precipitation are of great importance. This, of course, must always be studied in connection with the many factors modifying its efficiency, among which is that of run-off. The latter is largely controlled by porosity of soil together with topography. Measurements of rainfall have been made at Alpine and at Green Valley, about 35 miles to the southwest. The precipitation at both stations is of the same sporadic type and very similar in amount.

At Green Valley, the rainfall record for 14 years preceding 1929, gives an annual mean of 14.5 inches. Less than 7 inches fell in 1917 and 25.5 inches in 1920 (Fletcher, '28). Most of the rainfall occurs between June and October (Table I).

TABLE I. *Mean monthly and annual precipitation at Alpine for a period of 7 years and at Green Valley for 14 years*

Station	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Ave.
Alpine.....	0.17	0.38	0.67	0.40	0.85	1.76	2.53	2.35	2.50	1.19	0.70	0.96	14.46
Green Valley.....	0.63	0.08	0.33	0.28	1.42	1.95	1.23	3.28	1.96	1.56	1.12	0.17	14.02

The showers are nearly always sudden and rather local. Cloudbursts are of frequent occurrence. For example, in August, 1920, nearly 8 inches of rain fell in a few hours over a relatively small area. While this is an extreme case, it emphasizes the great loss of water due to run-off even on rather flat areas and especially on sloping and rolling lands. Such floods remove both soil and vegetation, leaving great gullies and covering other vegetation with unsightly soil deposits. Much moisture is dissipated, moreover, in light showers that do not increase the water content of the soil. Snowfall is light and the snow invariably melts within one or two days, the unfrozen soil readily absorbing the water. Hence a spring favorable for plant growth almost invariably follows a snowfall of any magnitude.

Very little rain falls during March and April when temperatures are favorable for renewed plant growth. This is, moreover, a season of high winds which further desiccate both plants and soil. Throughout the rest of the year, wind movement is so small as to be of little ecological importance.

The sunlight is intense because of the high altitude, cloudless skies, and dry atmosphere. Clear weather is a marked characteristic of the climate.

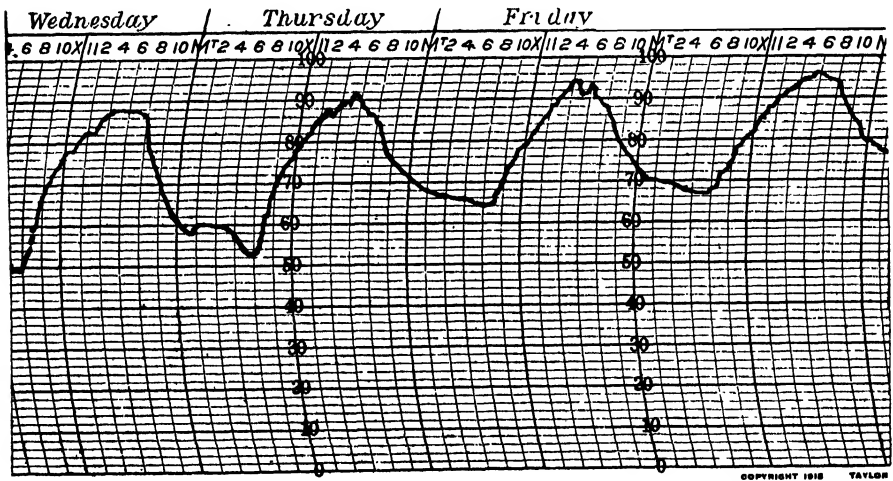


FIG. 10. Portion of a thermograph record during June showing the high temperatures of late afternoon and the relatively low night temperatures.

Approximately 75 per cent of the days are cloudless and only rarely do entirely cloudy days occur.

The frostless season usually extends from March 15 to November 15. The lowest temperature of any day during January and February of both 1928 and 1929, was 12° F., although by noon of these same days the temperature had risen to 60°. The average daily minimum temperature for these months was 31°, and the average daily maximum was 60°. The high variation in temperature from day to night (usually 30° and sometimes 60°)

is a marked feature of the climate. The sparse cover of vegetation, low humidity, and high altitude all contribute to the intense heating of the earth's surface by day and an equally rapid cooling at night. Summer temperatures (in shade) of 90° to 95° are common and sometimes temperatures of 100° to 104° are attained. Figure 10 shows a portion of a typical thermograph record for June. The average daily maximum and minimum temperatures at Alpine during 1927 and 1928 are shown in Table II.

TABLE II. *Average daily maximum and minimum temperatures at Alpine*

1928	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Ave. Maximum.....	66	57	71	70	81	93	85	79	78	76	76	
Ave. Minimum.....	32	28	38	43	50	61	61	57	52	46	40	
1929												
Ave. Maximum.....	59	60	62	79	85	92	86	86	90	78	56	54
Ave. Minimum.....	31	31	37	49	56	65	63	63	65	48	34	30

Few data are available on humidity. Psychrometer readings were taken in the grassland at Alpine, during two consecutive weeks in August and September (Table III).

TABLE III. *Relative humidity at Alpine, during August and September, 1929*

Time	August				September							
	27	28	30	31	1	2	3	4	5	6	7	8
7 A.M.....	69	90	89	74	65	67	49	76	85	76	80	76
10 A.M.....			50	46	40	38	41	48				
1 P.M.....	56	30	32	30			30	30	30	30	33	38
6 P.M.....	35	35	36	31	22	29	24	35	35	44		44
10 P.M.....	52	54	55	38	34	40	39	46	46	70	62	60

These figures show that the cold night air (7 A.M.) is fairly moist (49 to 90 per cent humidity), but that of the day, often as late as 10 P.M., is very dry. The day humidity was frequently between 25 and 35 per cent. During periods of drought it is probably lower. This is clearly indicated by losses from atmometers which were frequently 75 to 85 cc. daily.

LOCATION AND DESCRIPTION OF STATIONS

Four stations were selected to study carefully the vegetation and to measure the environmental factors under which it develops. In addition, permanent quadrats and exclosures were made in order to determine the responses of the plant cover to grazing and to protection from grazing.

One station was located on the Mitchell flat, 18 miles west of Alpine, at an altitude of 4,650 feet. This is one of the largest and highest flats in the

state, having a length of over 100 miles and a width of approximately 50 miles. The dominant grasses are *Bouteloua gracilis* and *B. hirsuta*. Vast areas are characterized by an open growth of yuccas, others by the bear grass (*Nolina*), and still others by cat's claw (*Acacia*) (Fig. 11).

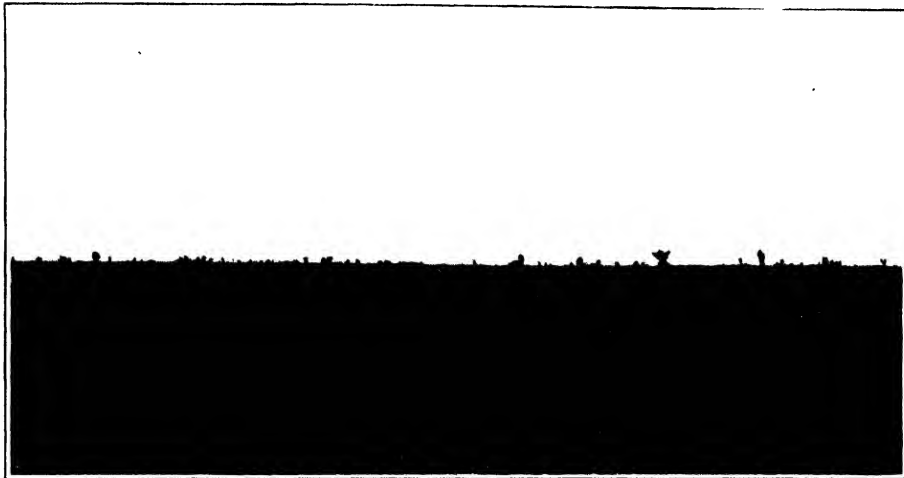


FIG. 11. Society of bear grass (*Nolina texana*) on the Mitchell flat in a cover of *Bouteloua gracilis* and *B. hirsuta*.

Another station, 15 miles south of Alpine, was located on the McIntyre ranch which is a tract of grassland covering 80,000 acres. The altitude of

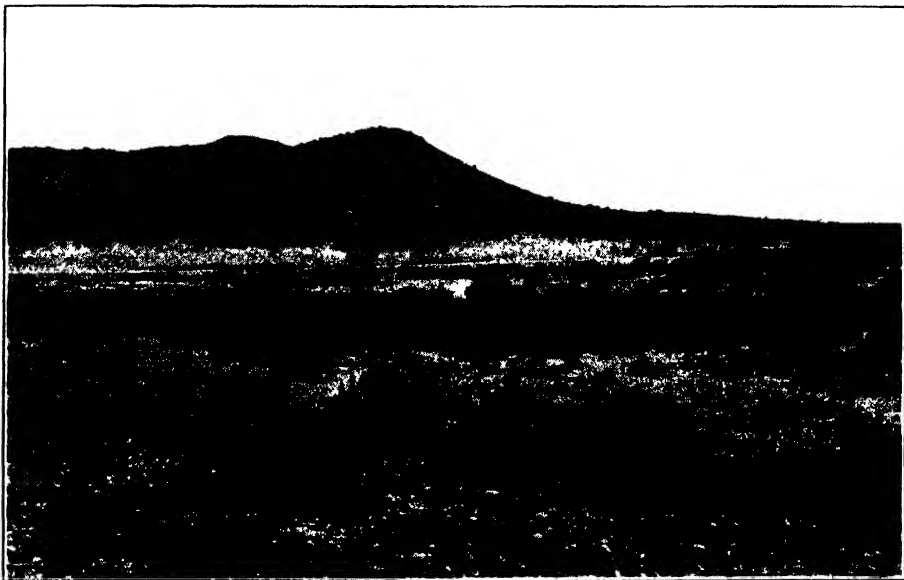


FIG. 12. Rolling hills with scattered cedars and flat valley with acacias and desert shrubs intermixed and alternating with the grasses. McIntyre station.

this station is 5,000 feet, and it differs from the preceding in several respects. The topography is much more irregular, being composed of rolling hills and rather flat valleys, often with deep arroyos (Fig. 12). Moreover, the entire region is surrounded by mountains. That run-off is high is indicated by the xeric short grasses. Outcropping rock ledges on the hills are covered with lichens and other pioneer vegetation of the xerosere. Here also occur scattered growths of piñon pine (*Pinus edulis*), red cedar (*Juniperus monosperma*), and scattered individuals of *Opuntia arborescens*. The dry water courses of the valleys are set off by narrow bands of evergreen oaks, *Quercus grisea*.

The third station was about two miles north of Alpine near Kokernott Springs. The altitude is approximately 4,400 feet, and the topography differs but little from that of the Mitchell station. This flat consists of about 100,000 acres. It is surrounded by mountains which rise abruptly 1,500 feet (Fig. 13). Although in general the short-grass type of vegetation prevails, the

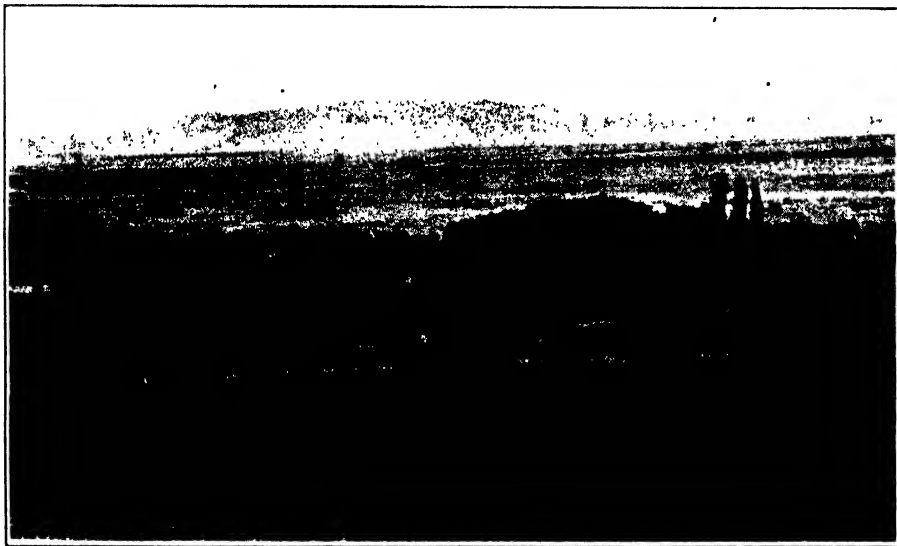


FIG. 13. General view of broad flats and surrounding mountains at Kokernott Springs. The springs are in the foreground concealed by deciduous trees.

adobe soil results in high run-off, and many types of desert scrub occur. Owing to the proximity to water, the region is greatly overgrazed, a condition that has probably long existed. In fact, much of the short-grass cover has been replaced by the more xeric *Scleropogon brevifolius*. *Acacia* scrub controls scattered areas as does also the spiny *Condalia* and other types of desert shrubs. The presence of hydric conditions about the springs is in striking contrast to the desert habitat 200 feet away. Cottonwoods and willows stand in sharp contrast to the adjacent xerophytes.

The Jackson-Harmon station was located 10 miles east of Alpine on a level

tract of land which was an ancient lake bed. This area lies at an altitude of 4,000 feet and is approximately 2.5 miles square. The clay soil has a high water-holding capacity, water runs in from the surrounding uplands and adds to the available supply. Consequently the vegetation is of the postclimax, tall-grass type, consisting chiefly of tobosa grass (*Hilaria mutica*) (Fig. 14).



FIG. 14. Tobosa-grass flat with *Plourensia* in the background on the Jackson-Harmon ranch.

Because of the great extent of the area and especially because of the lack of much taxonomic work in the region, no attempt has been made to describe the flora in detail (*cf.* Havard, '85; Bray, '01; Fletcher, '28). Attention has been focussed on the dominant and principal species and only those species are included that are of considerable importance in the composition of the plant cover.

THE MITCHELL FLAT

Vegetation

The vegetation of the Mitchell flat is characterized by three short grasses, viz.: *Bouteloua gracilis*, *B. hirsuta*, and *B. eriopoda*. Of these the first two are usually rather equally intermixed, *B. hirsuta* becoming more abundant on the sandier soils and *B. gracilis* increasing in importance on the heavier loams. *B. eriopoda* occupies areas of thinner soils and is always intermixed with varying amounts of the preceding species.

Owing to the low efficiency of the meager rainfall combined with persistent overgrazing, the grassy cover is far from continuous. Usually only about 10 per cent of the soil is occupied by the grasses, thus leaving much sur-

face exposed (Fig. 15). The mats or tufts of grass are only 3 to 4 inches tall, those of *B. eriopoda* differing from the others in being less leafy at the base and provided with short stolons which root at the nodes. Flower stalks are relatively sparse; those of *B. hirsuta* are shortest (4 to 6 inches), *B. gracilis* is somewhat intermediate, while those of *B. eriopoda* are normally 8 to 12 inches tall. *Muhlenbergia monticola* and *Aristida* sp. are the only other grasses of any ecological significance and their rôle is unimportant.

If sufficient moisture is available, the grassy cover becomes green in March, and after a period of only 6 weeks flower stalks are put forth and blossoming begins. But usually the early growth is followed by a period of



FIG. 15. View of vegetation at the Mitchell station, showing the open nature of the plant cover and the enclosures where quadrat studies were made.

semidormancy preceding the summer rains, when the plants cure more or less completely on the ground. Growth in the autumn is usually controlled by temperature since, ordinarily, sufficient water is available. Thus the grasses remain green until the middle of November, and grazing continues throughout the winter. A heavy cover of snow is practically unknown.

The landscape, however, is conspicuous not because of the grasses but owing to various large, non-grassy species. Chief among these are the yuccas, the bear grass, and *Koeberlinia*. The most conspicuous plant over vast areas is *Yucca elata* (Figs. 3 and 15). This plant develops in two growth forms, one a rosette, and the other producing a trunk, often 8 to 10 feet in height and 6 inches in diameter. The sharp-pointed leaves are about $\frac{1}{2}$ inch wide and 12 to 18 inches long, with white, thread-like fibers along the margins. The dead leaves persist for several years on plants that produce trunks. They

hang down about the trunk giving the plants much the appearance of palms. The blossoms are produced on long stems 4 to 5 feet tall which protrude from the crown of the plant. The rosette type usually produces only one flower stalk, but individuals that have developed trunks may produce 8 to 10.

These plants are well adapted to withstand drought. During the summer of 1929, which was so dry that most of the other vegetation was dead or dormant, the yucca blossomed as usual and produced an abundance of seed. When the plants are shredded they make good food for live stock. Cattle readily eat them and the food value is high.

The bear grass, *Nolina texana*, is widely distributed over other portions of the flat (Fig. 19). It grows in dense clumps or tufts from 1 to 2 feet in diameter, and produces from its crown many slender, grass-like leaves, 1 to 2 feet long. In cross section, the leaves are more or less triangular, about $\frac{1}{4}$ inch in diameter, and remain green all winter. They are very tough and fibrous, and have been used by the Indians for basketry, and by white men to make brooms. During the winter the cattle chew the leaves to extract the juice but can not break the fibers. This gives the plant a very ragged appearance in the spring. The small blossoms are borne in dense clusters in the tuft of leaves, the flower stalk being shorter than the leaves.

A third type of coarse subdominant is represented by *Koeberlinia spinosa*. This shrub is commonly known as "all thorn" on account of its very thorny nature. It attains a height of 6 to 8 feet, but produces no leaves. The branches are green during the entire year and do the work of leaves. The blossoms are very small and form in dense clusters. The black fruits are about $\frac{1}{4}$ inch in diameter.

Various species of flat-leaved opuntias (including *O. lindheimeri* and *O. macrocentra*) occur scattered throughout the area. Single individuals frequently occupy 3 to 5 square feet, but they are usually isolated and, although conspicuous, they are never abundant. A low growing species of *Acacia* (*A. roemeriana*) and isolated clumps of *Ephedra trifurca* are sometimes found on dry knolls, but neither is of much ecological importance. Other subdominants are as follows:

Aristida sp.
Asclepias latifolia
Asclepias verticillata
Astragalus mollissimus
Clematis drummondii
Croton corymbulosus
Engelmannia pinnatifida
Eriogonum annuum
Gutierrezia glomerella
Gutierrezia texana

Linum berlandieri
Melampodium cinereum
Muhlenbergia sp.
Perezia nana
Ratibida columnifera
Salsola pestifer
Senecio filifolius
Thymophylla aurea
Tragia ramosa

None of the preceding form conspicuous societies since the grass cover is very pure. They are usually found as more or less isolated individuals. Almost the entire water supply is utilized by the grasses and the conspicuous societies of yuccas and others already described, leaving little for the lesser subdominants.

Environment

In considering the environmental factors, the texture and structure of the soil in relation to their influence upon the absorption and retention of water are of major importance.

The soil consists of a clay loam that extends to a depth of about 18 inches. A mechanical analysis of the first foot gave, in addition to 14.2 per cent coarse gravel, the percentages of the particles of different sizes shown in Table IV.

TABLE IV. *Mechanical analysis of soil of the Mitchell flat*

Fine gravel	Coarse sand	Medium sand	Fine sand	Very fine sand	Silt	Clay
3.2	5.4	4.7	17.0	23.1	14.3	32.3

It may be noted that approximately one-third of the soil is clay and that the proportions of silt and fine sands are also large. This fine-textured soil is so compact that water is slowly absorbed and much of the rainfall is lost in run-off. The hygroscopic coefficients of the first, second, and third feet are 10.5, 9.8, and 8.3 per cent respectively. The hygroscopic coefficient, which is perhaps the most dependable of all of the soil constants, is a good index of the water-holding capacity. The latter was found to be 48 per cent for the first six-inch layer (Hilgard method), 55 for the second, and 56 for the third. The surface 18 inches of fine-textured soil has a sufficient water-holding capacity to retain all of the moisture, even during periods of unusual rainfall, aside from the run-off due to its compactness. Like all of the soils of the flats, its pH reaction is neutral.

Below 18 inches, but sometimes at a depth of 3 feet, there occurs a layer of subsoil that is almost always powdery dry, very hard, and extremely high in lime. This underlies the surface soil to a depth of several feet. Actual determinations showed a calcium carbonate content of 31.5 per cent in the second foot and 42 in the third. Root development is practically confined to the surface soil; the few roots that enter the calcareous layer soon die and decay. Like all non-alkali soils of dry climates, the potential fertility is high, and water is the major factor limiting plant production.

Water-content determinations were made at approximately 15-day intervals throughout the growing seasons of 1927, 1928, and 1929. Samples of 300 to 400 grams were obtained in duplicate by means of a 1.5-inch soil auger, to depths of 6, 12, and 18 inches respectively. No moist soil occurred at greater depths at any of the stations, except in the old lake bed.

Water content during 1927 is shown in figure 16. Even casual examination shows that no water was available for growth after the middle of April until late in August. This corresponds with the behavior of the vegetation, the grasses remaining in a semi-dormant condition throughout the period of drought. It seems probable that light showers moistened the surface soil and

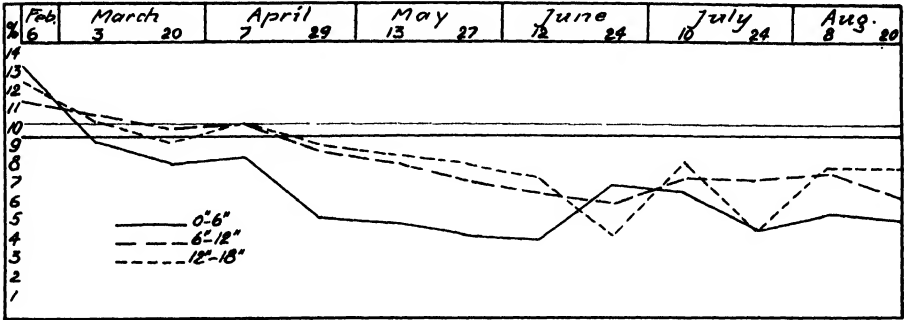


FIG. 16. Water content at the Mitchell station during 1927. Here, as in the following figures, the light horizontal line is the hygroscopic coefficient of the first foot, the heavy one of the second.

furnished some growth-water between the periods of sampling. The writer is of the opinion that water may also be absorbed from the soil by the well developed network of grass roots even after it is reduced below the hygroscopic coefficient. It seems probable that moisture may be lost as vapor from these warm, dry soils to depths of 18 to 24 inches, thus accounting in part for their very low water content.

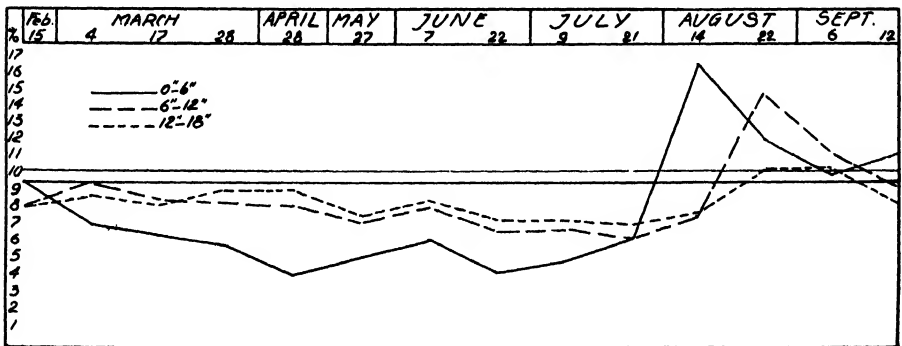


FIG. 17. Water content at the Mitchell station during 1928.

Conditions were more xeric during the spring of 1928, but somewhat less severe below the surface six inches during the summer (Fig. 17). By July 21, good rains had refreshed the parched vegetation which immediately began life anew. The effects of light showers in replenishing the water of the surface soil is well shown during the season of 1929 (Fig. 18).

The low water content of soil is reflected in the xeric vegetation, the driest type of grassland in the area occurring on this flat. Coupled with low water content there occurred high soil temperatures and great evaporation.

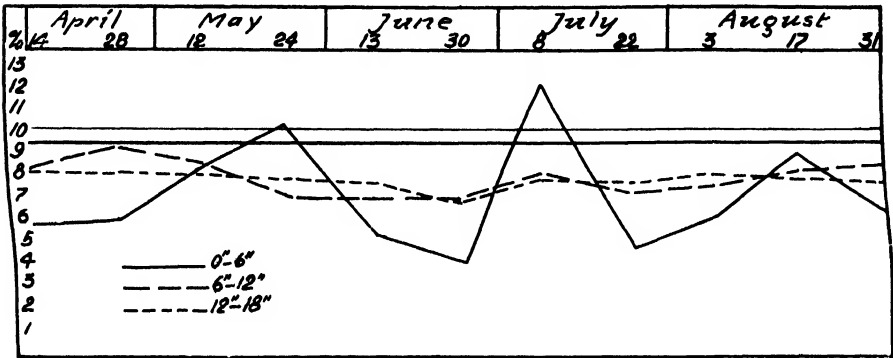


FIG. 18. Water content at the Mitchell station during 1929.

Soil temperatures were measured at depths of 2 and 12 inches. Readings were usually made between 4 and 5 P.M. These records are shown in Table V.

TABLE V. Soil temperatures in degrees Fahrenheit on the Mitchell flat at depths of 2 and 12 inches

1927	At 2 in.	At 12 in.	1928	At 2 in.	At 12 in.	1929	At 2 in.	At 12 in.
Jan. 9.....	52	39	Feb. 15.....	64	52	Apr. 14.....	85	68
Feb. 6.....	65	58	Mar. 17.....	78	60	Apr. 28.....	94	76
Mar. 3.....	78	62	Mar. 28.....	88	70	May 12.....	100	78
Mar. 20.....	64	58	Apr. 28.....	104	76	May 24.....	92	74
Apr. 10.....	90	73	May 27.....	82	76	June 13.....	94	84
Apr. 29.....	98	74	June 8.....	104	82	June 30.....	102	84
May 13.....	94	74	June 22.....	116	90	July 8.....	78	78
May 27.....	104	84	July 9.....	106	86	July 22.....	100	88
June 12.....	100	86	July 21.....	96	84	Aug. 3.....	106	88
June 24.....	106	84	Aug. 4.....	80	78	Aug. 17.....	98	82
July 10.....	110	86	Aug. 22.....	88	78	Aug. 31.....	88	82
July 24.....	98	84	Sept. 7.....	88	78			
Aug. 8.....	105	92	Sept. 12.....	96	84			
Aug. 20.....	86	82						

The lowest recorded soil temperature (39° F.) is at 12 inches on January 9. This is in agreement with the fact that the soil seldom freezes below a depth of one inch. Early in February the temperatures within the root zone ranged between 52° and 65° and were sufficiently high to promote growth. Surface temperatures of 100° or above occurred late in April or in May, and they ranged much higher (maximum 116°) during the dry, hot days of June. At 1 foot the temperatures were also very high (85° to 92°). It is entirely probable that even higher temperatures occurred on days when readings were not taken. The air temperature frequently reached its

maximum between 5 and 6 P.M., and the surface soils also may have been warmer somewhat later than 5 P.M.

Evaporation was measured during the growing season by means of Livingston's white, cylindrical atmometers. These were standardized instruments with non-absorbing devices and were used in duplicate at each of the several stations. The evaporating surface of the cup was placed 15 to 20 cm. above the surface of the soil. The average daily readings, corrected to correspond with those of the standard cups, are presented in Table VI.

TABLE VI. *Average daily evaporation from Livingston's cylindrical atmometers, on the Mitchell flat*

1927	Loss in cc.	1928	Loss in cc.	1929	Loss in cc.
Apr. 28 to May 13 . . .	60	May 27 to June 8 . . .	65	Apr. 26 to May 12 . . .	33
May 13 to May 27 . . .	42	June 8 to June 22 . . .	78	May 12 to May 24 . .	19
May 27 to June 12 . . .	29	June 22 to July 9 . . .	79	May 24 to June 13 . .	29
July 24 to Aug. 8	37	July 9 to July 21 . . .	38	June 13 to June 30 . .	25
Aug. 8 to Aug. 20	45	July 21 to Aug. 4 . . .	12	July 8 to July 22 . . .	63
Aug. 20 to Sept. 2	49	Aug. 4 to Aug. 22 . . .	9	July 22 to Aug. 3 . . .	42
		Aug. 22 to Sept. 7 . . .	11	Aug. 3 to Aug. 17 . . .	27
				Aug. 17 to Sept. 6 . . .	27

The continuous record for 1928 shows a very high evaporation rate from late in May until the rainy season, beginning in July. A mean daily loss of 65 to 79 cc. indicates extremely xeric conditions and is almost twice as great as the average, for example, on the short-grass plains of Colorado (*cf.* Weaver, '24). During the rainy season, the average daily losses scarcely exceeded 30 cc., in this respect approaching very closely those of true prairie of eastern Nebraska.

During 1927, the evaporation was not so extreme but it was relatively high. Evaporation during 1929 was comparatively low (19-33 cc.) from April to July; it reached a maximum (63 cc.) during midsummer, and then again fell to 42-27 cc. High evaporation desiccates the vegetation at a time when the soil is very dry. Hence only a relatively scanty plant population of xeric species can endure. The development of the vegetation is further retarded by continuous grazing and trampling, and the wonder is, not that it is greatly injured, but that it does not entirely disappear.

Root Distribution

The depth of root penetration of perennials in these arid soils is controlled by the depth to which the soil is moistened. The lateral spread of roots is often well developed thus increasing the absorbing area. Hence the surface cover gives little information as to the occupancy of the soil by the roots, and the structure and distribution of the vegetation will not be clearly understood without some knowledge of the underground parts. Consequently studies on root distribution were made at each of the stations. A grama grass, a *Nolina*,

a cactus, and a yucca were examined at Mitchell Flat. Owing to the compactness and usually very dry condition of the soil at all the stations, this work was difficult and many details were not secured. A clear idea of the general root relations was, however, obtained.

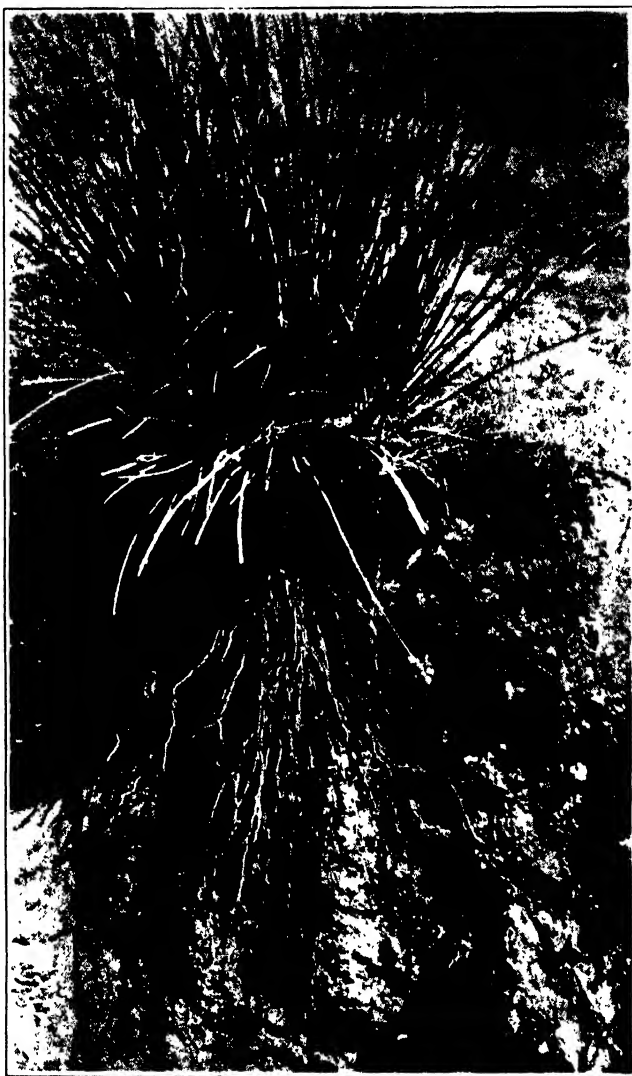


FIG. 19. A clump of bear grass (*Nolina texana*) showing about 2.5 feet of the coarse root system.

The small clumps of *Bouteloua gracilis*, about 2 in. in diameter, gave rise to very numerous fine roots. A few extended to the layer of lime at about 30 inches, but the bulk of the root system was in the surface 18 inches of soil.

Judging from the abundance of branching, most of the absorption took place in the surface foot. Here the short laterals (0.5 inch or less in length) occurred at the rate of about 20 to 25 per inch of main root, and quite filled the soil. Moreover, the lateral spread was 6 to 8 inches from the base of the plant at a depth of 4 inches. Thus the roots of this dominant occupy an area below ground that is 30 to 50 times greater in extent than that of the small mat from which the roots arise.

The plants of *Nolina* consist of coarse tufts 6 to 12 inches in diameter that give rise to a great cluster of coarse, fibrous roots (Fig. 19). These are frequently 3 or 4 mm. in diameter, almost throughout their course. A few reached a depth of 39 inches but the working level did not exceed 2 feet. About two-thirds of the roots penetrated more or less vertically downward or downward and outward. The rest ran obliquely and seldom deeper than 18 inches, after which many again turned upward and ended 6 to 12 inches below the soil surface. The lateral spread was frequently 4.5 feet. Branches were sparse. Some entire roots were without laterals, and where they did occur on others they were only 2 to 4 inches long. Each root was clothed with a spongy cortex. There were some indications that fine, absorbing roots were produced during the rainy season and dried up during drought, but this needs further study.

A species of *Opuntia* with 8 flat lobes, 15 inches high, and a basal diameter of 1.5 inches, was excavated. There were 14 fleshy roots that penetrated vertically to 8 to 12 inches depth and were finely branched near their tips. The remainder of the root system, consisting of 4 major roots, spread widely in the surface 3 inches of soil. These fleshy roots were about 5 mm. in diameter and varied in length from 5 to 10 feet. The shorter ones were profusely branched throughout their entire extent, the longest one most abundantly near its end. The major branches were frequently 1 to 5 feet long and sublaterals were abundant. Thus the cactus is well equipped to absorb in the shallower soil and accumulate water to be used during times of drought (*cf.* Cannon, '11).

The specimens of *Yucca elata* had stems 3.5 inches in diameter and 3 feet high. The caudex under ground was of approximately the same diameter (Fig. 20). It ended abruptly when it reached the calcareous layer at 2.5 feet. The main roots arose from the caudex at intervals of about an inch. They ran horizontally outward to distances of 5 to 10 feet. Many ended at the same soil level as their origin; none penetrated deeper than the caudex, and many ran outward and upward. These roots were 3 to 5 mm. thick and covered with a spongy cortex. They were poorly branched, sometimes several feet of root-length being free from laterals. Usually the length of branches did not exceed 4 to 12 inches (*cf.* Markle, '17; Weaver, '19).

From these data, it may be concluded that the vegetation at this station absorbs all of its water supply in the surface 2.5 or 3 feet of soil and that absorption is most vigorous in the first foot.

Studies in Overgrazing

At each of the stations studies were made of the effects of grazing. Ex-closures, chart and clipped quadrats were used in these investigations. The

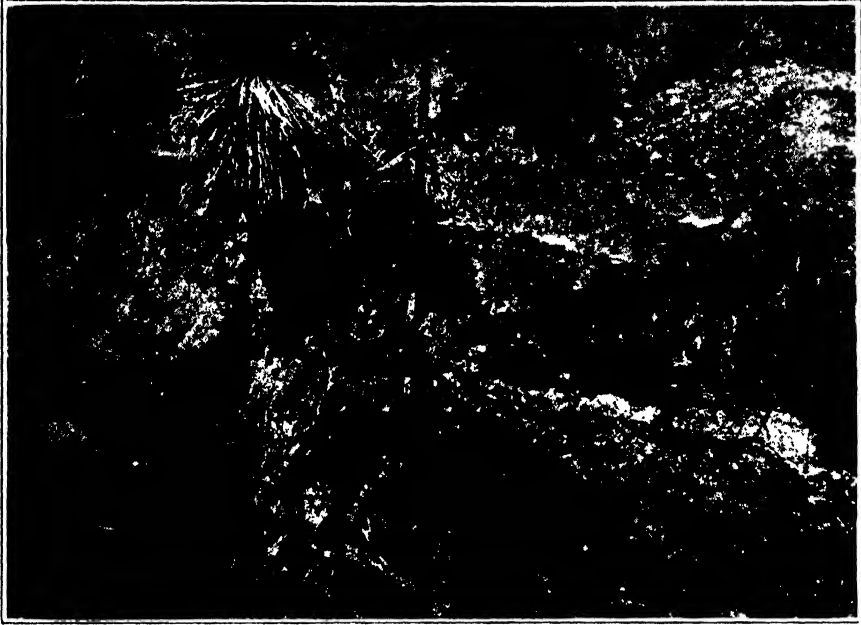


FIG. 20. Partially excavated caudex and root system of *Yucca elata* showing also some of the coarse, main horizontal roots.

exclosures at each station contained an area of three square rods (approximately 76 square meters), cattle being excluded from the first square rod (approximately 25 square meters) in 1927, the second in 1928, and the third



FIG. 21. Detail of vegetation on the unprotected range at the Mitchell station. Ninety-four per cent of the soil is bare.

in 1929 (Clements, '20). Since the areas were adjacent, a comparison of the vegetation with that of the open range could readily be made after one, two, and three years of protection (Fig. 15). Great care was exercised in

selecting the site for the exclosures so as to represent typical conditions. Permanent quadrats both inside and outside the exclosures were annually charted at the end of the growing season. The vegetation from each quadrat was then clipped, air dried, and weighed. In charting, the basal area rather than that of the spreading tops of the plants was delimited (*cf.* Sarvis, '23). In this manner the effects of various periods of protection upon vegetative propagation, production of flower stalks and seeds, and establishment of seedlings, as well as the increase in forage production, were determined.

A representative quadrat in the unprotected range on the Mitchell flat is shown in figure 21. The sparse growth of the short grama grasses, which covers only 6 per cent of the area, and the high percentage of bare soil, may be plainly seen. The marked development of the grasses after one, two, and

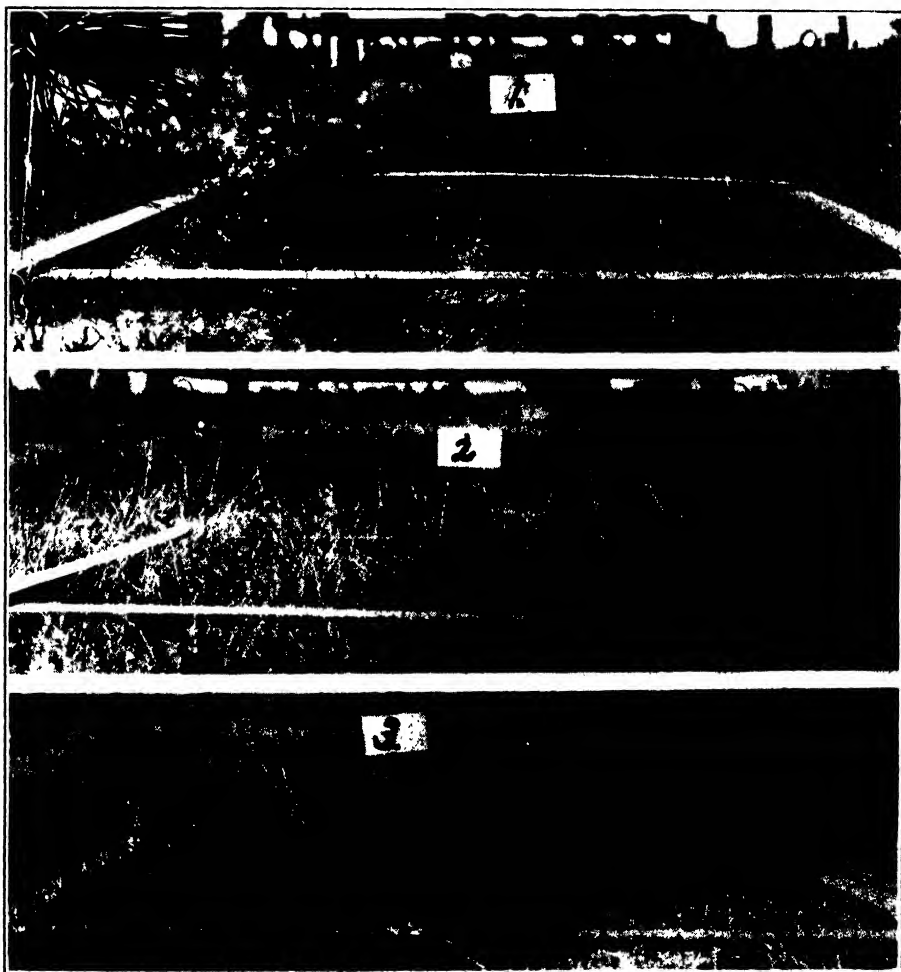


FIG. 22. Representative quadrats at the Mitchell station protected 1, 2, and 3 years respectively.

three years of protection is also evident (Fig. 22). Figure 23 shows an unprotected quadrat; one within the enclosure is also included for comparison.

Differences in the number and size of plants under the two conditions, the

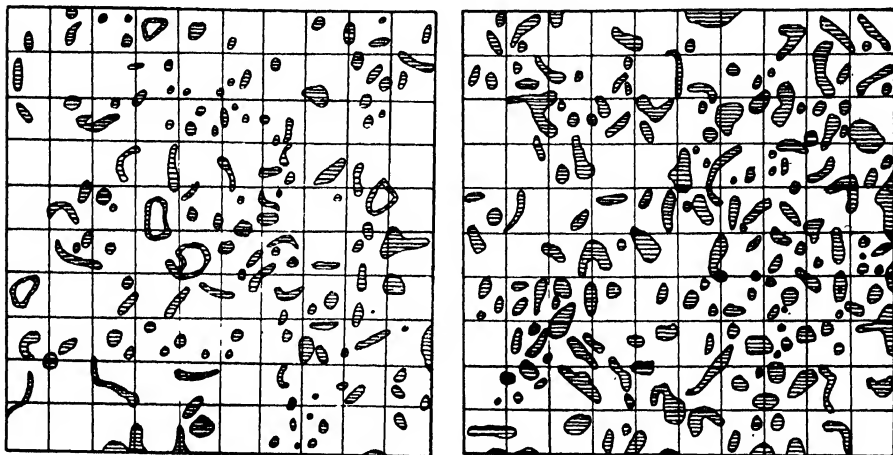


FIG. 23. A typical grama grass quadrat outside the enclosure (left), and one that has been protected two years.

per cent of ground cover, number of seed stalks, yield of dry matter, and percentage increase in yield are shown in Table VII.

TABLE VII. *Data from grazed and protected quadrats on the Mitchell flat*

Treatment	No. of plants	Size of mats, etc. sq. cm.	Percentage of cover	No. seed stalks	Yield dry matter, gr.	Per cent increase in yield
Unprotected	152	.4	6.2	134	11	0
Protected 1 yr.	241	.42	10.0	198	34	209
Protected 2 yrs.	176	.75	13.3	246	52	372
Protected 3 yrs.					90	718

This table shows that there is a great increase in the number of plants after a single year of protection, but a decrease the second. By the end of the first year the underground parts of the broken mats gave rise to many new shoots that were sufficiently distant from the others to be listed as individuals. But after two years of protection these, in many cases, had consolidated with the main clumps. Moreover, numerous seedlings lived but one year. The size of the clumps steadily increased and at the end of the second season was almost doubled. This is indicated by a great increase in total ground cover. A progressive and marked increase in the number of seed stalks also occurred. The yield in dry matter increased 209 per cent the first year, 372 the second,

and 718 the third. Unfortunately time was not found to determine the number of plants, etc., at the end of the third year of protection. The actual forage production is shown in figure 24.

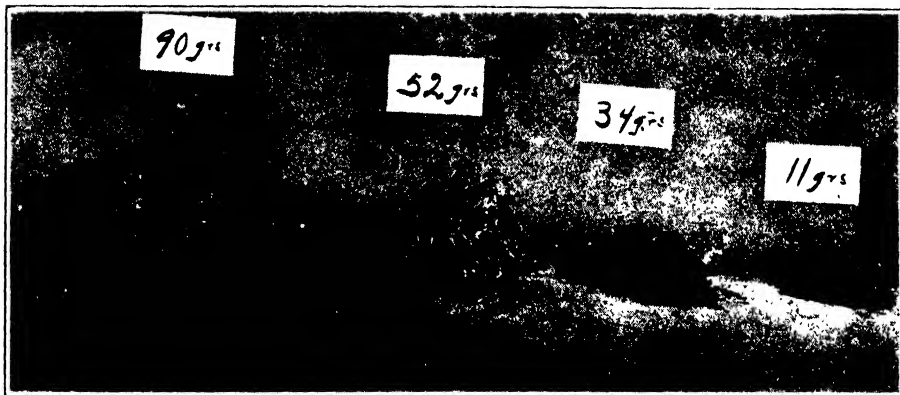


FIG. 24. Average yields per square meter on the Mitchell flat without protection (right), and with protection for 1, 2, and 3 years respectively.

McINTYRE STATION

Vegetation

Short grasses dominate most of the extensive area of the McIntyre station. Conditions for their growth are much more favorable than on the Mitchell flat. This is shown by the almost complete absence of *Bouteloua*

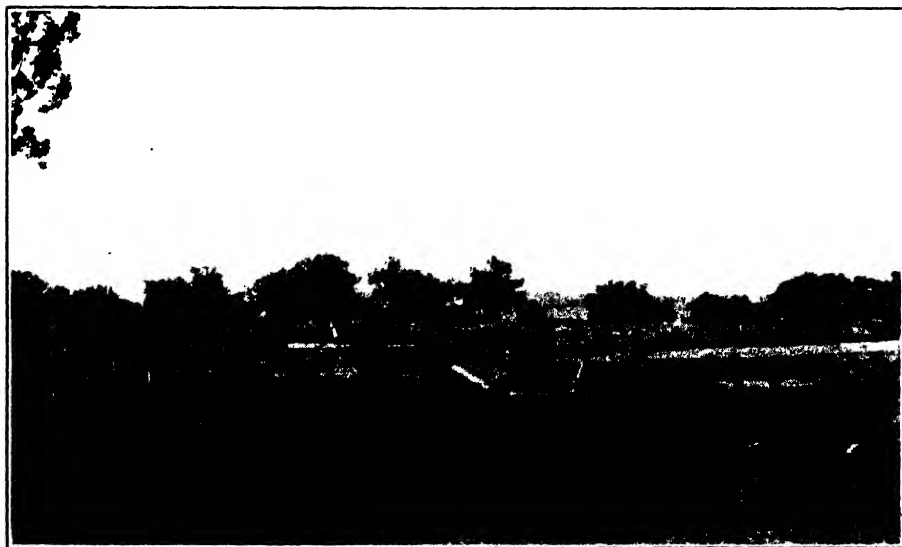


FIG. 25. Cover of *Bouteloua gracilis* and *B. hirsuta* near exclosures at the McIntyre Station.

eriopoda and by the better development of *B. gracilis* and *B. hirsuta*. The grassy cover is still very open, however, and only 10–15 per cent of the soil surface is occupied (Fig. 25). The cover is continuous over the undulating hills and broad valley, being much thinner on the steeper uplands due to loss of precipitation by run-off, and is somewhat better developed wherever surface water runs in and adds to the scanty supply (Fig. 12).

On the dry uplands where the soil is thin and the rocks often outcrop, there occurs an open stand of red cedars (*Juniperus monosperma*). These are also found intermixed with the oaks along the lowland washes, or alone mark the course of the broken soil along arroyos. The cedars are usually accompanied on the uplands by a very small mixture of piñon pines (*Pinus edulis*), which on limestone hills eastward are nearly as numerous as the cedars. This woodland represents an extension of the Piñon-Juniper woodland which is in contact with the grasslands to the northwest (Bray, '01; Shantz and Zon, '24).

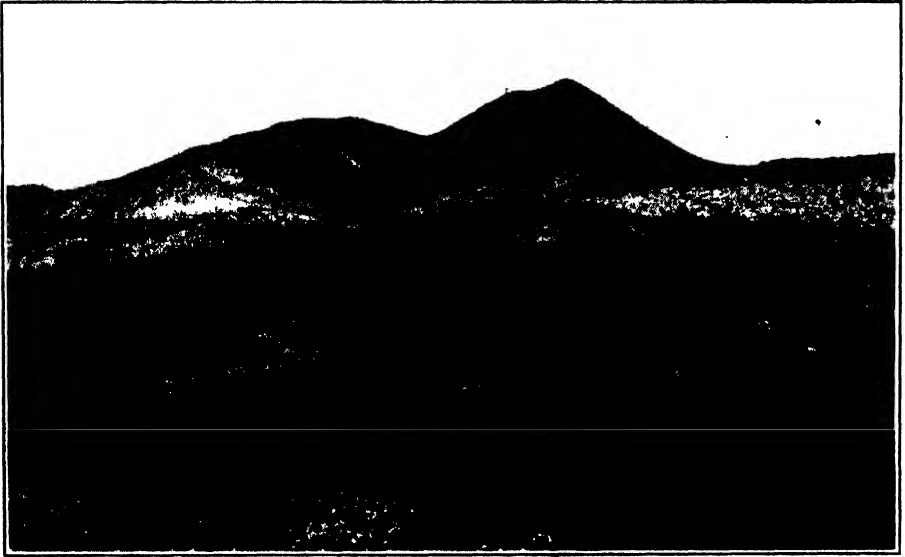


FIG. 26. Oak woodland (*Quercus grisea*) alternating with grassland. The oaks benefit from the run-off waters from the slopes. Dense clumps of bear grass (*Nolina texana*) occur in the foreground.

The junipers are low, scrubby, gnarled trees usually about 25 feet tall. The diameter of the trunk of fairly mature trees varies from 1 to 3 feet at the base. The trunk divides into numerous large branches, often just above the soil surface, and leafy branches are so near the ground that the tree takes on a bushy aspect. The pines are tree-like in habit but seldom exceed 18 inches in diameter and 35 feet in height. The cedars sometimes grow in small clumps but more usually, like the pines, in very open, scattered stands. Beneath the trees there is an accumulation of needles and other debris. This,

with decreased light and increased competition for water, places the grasses at a disadvantage, but they occupy the soil of the open places between the trees.

An evergreen oak (*Quercus grisea*) forms extensive growths along the eroded waterways where run-off water accumulates and greatly increases the moisture supply. These vary from narrow ribbons to belts of open woodland a quarter of a mile wide. Clumps and small groves also occur (Fig. 26). From these vantage places the trees migrate up the lower slopes, especially the northern ones, scrubby specimens sometimes reaching the crests. These much-branched, low-growing trees seldom exceed 18 inches in diameter and 20 feet in height. The growth is nearly always so open that the grass carpet is scarcely interrupted, the better water supply being reflected in the herbaceous as well as the tree vegetation. *Quercus emoryi* also occurs sparingly as well as a few trees of *Arbutus texana*.

A conspicuous species of the better soil is the cane cactus (*Opuntia arborescens*). This shrubby plant is often 5 to 7 feet tall, but the individuals are widely scattered and of little importance ecologically. The cat's claw, a species of *Acacia*, occurs in open, scattered stands along the lower slopes of the hills. These thorny shrubs are usually 3 to 4 feet high but are never of sufficient density to interrupt the grassy cover.

In addition to the *Opuntia* and *Acacia*, numerous other shrubby and herbaceous societies occur. The most important of these are as follows:

Shrubs

Acacia farnesiana
Clematis drummondii
Fallugia paradoxa

Odostemon fremontii
Rhus trilobata

Herbs

Anisolotus wrightii
Anthericum torreyi
Argemone platyceras
Astragalus mollissimus
Asclepias arenaria
Asclepias nummularia
Berlandiera lyrata
Croton corymbulosus
Eriogonum tenellum
Gutierrezia texana
Lepidium sp.
Lesquerella fendleri

Marrubium vulgare
Nuttallia nuda
Opuntia arborescens
Pentstemon acuminatus
Pentstemon torreyi
Plantago purshii
Senecio filifolius
Tragia ramosa
Tribulus terrestris
Verbena pinnatifida
Vernonia marginata
Yucca elata

Environment

Many types and gradations of soil undoubtedly occur in a region with such diversified topography. Since the chief interest was in relation to grasslands, soil profiles were examined and analyses made in a representative

area of short grasses free from woody or shrubby vegetation. Here the soil was fairly uniform to a depth of 4 feet. Analysis of the surface foot is shown in Table VIII.

TABLE VIII. *Mechanical analysis of soil of the McIntyre station*

Fine gravel	Coarse sand	Medium sand	Fine sand	Very fine sand	Silt	Clay
3.5	3.4	2.7	13.9	36.7	18.7	21.1

A high amount of gravel (52 per cent) insured a fairly good water penetration and reduced loss by run-off. Seventy-seven per cent of the soil consists of particles of small size, varying from very fine sand to clay, which gives the soil a good water-holding capacity. This was found to be 47, 53, and 51 per cent for the 6, 12, and 18 inch layers respectively. Continuous soil

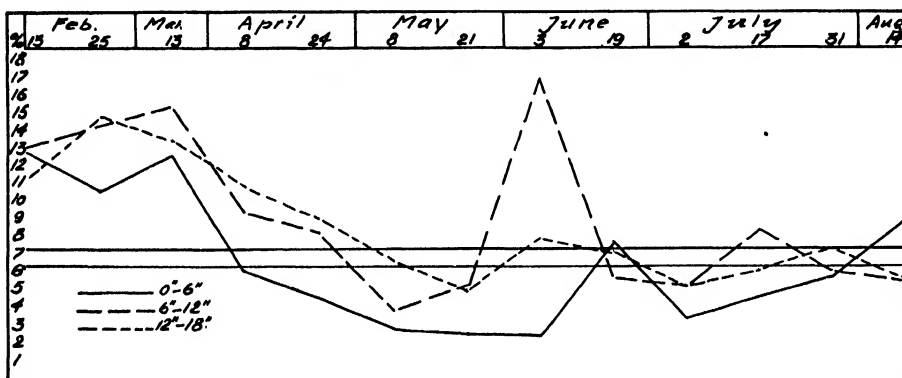


FIG. 27. Water content at the McIntyre station during 1927.

sampling showed that water did not penetrate beyond 3 feet. Owing to the high gravel content, the hygroscopic coefficients are relatively low—6.6, 7.5, and 7.4 respectively, for the three first 6-inch layers. The soil was neutral and only traces of lime occurred.

Water-content determinations during 1927 show that while periods of severe drought occurred, conditions as a whole were much more favorable than on the Mitchell flat (Fig. 27). During 1928, conditions were somewhat

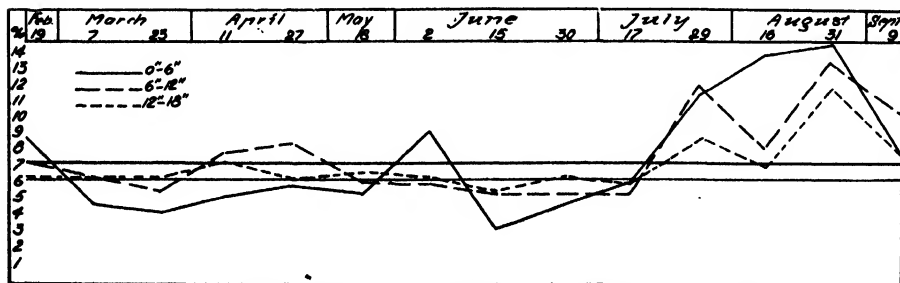


FIG. 28. Water content at the McIntyre station during 1928.

similar, although a plentiful supply of soil moisture was available after July 17 (Fig. 28). The following year was one of continuous drought, and from April to August the water content exceeded the hygroscopic coefficient only two or three times (Fig. 29). A study of the root systems of various species showed that roots occurred beyond the depth of soil sampling, and it is possible that some absorption was going on below 18 inches.

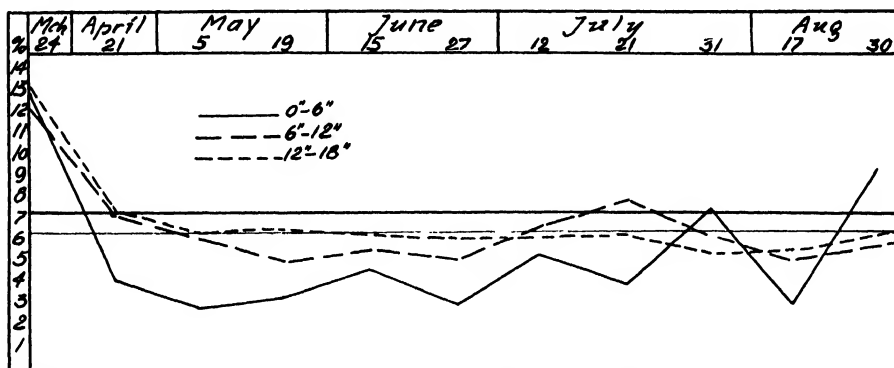


FIG. 29. Water content at the McIntyre station during 1929.

Soil temperature was measured as on the Mitchell flat, during a period of three years. The data are so nearly like those already given for the Mitchell flat that they need not be included.

Evaporation at the two stations varied much more than soil temperature. This was primarily due to the local nature of the rainfall and its effect upon humidity. The usual high rates of evaporation during dry periods and the more moderate ones in the rainy season are shown in Table IX.

TABLE IX. Average daily evaporation, from Livingston's cylindrical atmometers, at the McIntyre ranch

Date, 1927	Loss in cc.	Date, 1928	Loss in cc.	Date, 1929	Loss in cc.
Apr. 24 to May 8 . . .	53	May 18 to June 2 . . .	53	June 27 to July 12 . . .	55
May 21 to June 3 . . .	41	June 2 to June 15 . . .	85	July 12 to July 21 . . .	67
July 31 to Aug. 4 . . .	36	June 15 to June 30 . . .	77	July 21 to July 31 . . .	40
Aug. 4 to Aug. 30 . . .	44	June 30 to July 17 . . .	85	July 31 to Aug. 17 . . .	29
		July 17 to July 29 . . .	32	Aug. 17 to Aug. 31 . . .	19
		July 29 to Aug. 16 . . .	30	Aug. 31 to Sept. 5 . . .	27
		Aug. 16 to Aug. 31 . . .	20		
		Aug. 31 to Sept. 9 . . .	33		
		Sept. 9 to Oct. 4	26		

Root Distribution

The root systems of the two dominant grasses, also of *Opuntia arborescens*, and of a young juniper were examined at this station.

Bouteloua gracilis penetrated 6 inches deeper (36 inches) at this station

than on the Mitchell flat. The working level was also somewhat greater, but as before the most profuse branching and greatest absorbing area were found in the surface 18 inches of soil.

The roots of *Bouteloua hirsuta* reached a maximum depth of 30 inches but they were poorly branched below 18 inches. The working level was also shallower, being only 12 inches. But in the surface foot the roots spread widely, reaching a maximum lateral distribution of 3.5 feet. This was about one foot greater than for *B. gracilis*. Within an area of 4 square feet, of which the small tuft of grass formed the center, the soil was thoroughly occupied. Within this area to a depth of a foot, laterals $\frac{1}{4}$ to 1 inch long occurred at the rate of 25 per inch of main root, thoroughly ramifying the soil.

A plant of *Opuntia arborescens*, 2.5 inches in diameter and 3.5 feet high, was examined. From the base of the stem there arose 11 large, fleshy roots. These ranged from 12 to 18 mm. in diameter throughout the first 10 to 14 inches of their course, after which they tapered rapidly into fine, well branched roots. Seven of the roots ran rather vertically or somewhat obliquely downward, mostly to the second or third foot level, but one reached a depth of 40 inches. Four ran outward in the surface soil in a horizontal direction to about 4 feet, but one extended laterally to a distance of 10 feet, only 3 or 4 inches below the soil surface. All of its branches were superficial, the longest occurring near its end. Lateral branches, except on the fleshy portions of the roots where there were none, were 3 to 12 inches long and occurred at the rate of 6 to 8 per foot. Thus a single plant absorbed water to a distance of 5 or more feet in all directions from its base and especially in the surface 20 inches of soil (*cf.* Markle, '17).

A specimen of *Juniperus monosperma* was examined. It was 14 inches tall and $\frac{1}{2}$ inch in diameter, but approximately 35 years old, and possessed a strong taproot $\frac{1}{2}$ inch thick that ran vertically downward to a depth of 3.5 feet. Large lateral branches were numerous, most of them originating at the 4 to 18 inch level. These penetrated outward and downward often at angles of 30° to 45° and to a distance of 2 to 3 feet from the base of the plant. A few again turned upward to within 6 inches of the soil surface. The older portions, especially within a circumference of 2 feet of the plant, were well branched, laterals 1 to 3 inches long occurring at the rate of about 5 per inch. On the distal portion of the roots, branches were both fewer and shorter. Here, as in the preceding species examined, root depths were not great (3.5 feet or less), and the greatest root distribution and maximum absorption occurred in the surface two feet of soil. This small tree grew 100 feet from a very large one. The great spread of roots of large trees was indicated by the fact that a few roots of the old juniper were found in the trench at a depth of about 2 feet.

Studies in Overgrazing

The better conditions for plant development at the McIntyre station as compared with the Mitchell flat are revealed in the growth of grasses in the

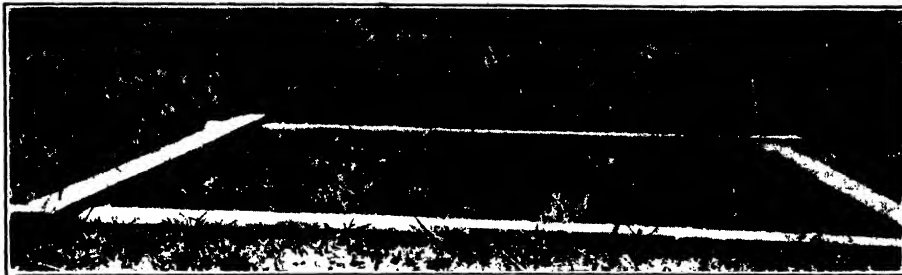


FIG. 30. Detail of vegetation on the unprotected range at the McIntyre station. The grama-grass cover is very open but less so than on the Mitchell flat.

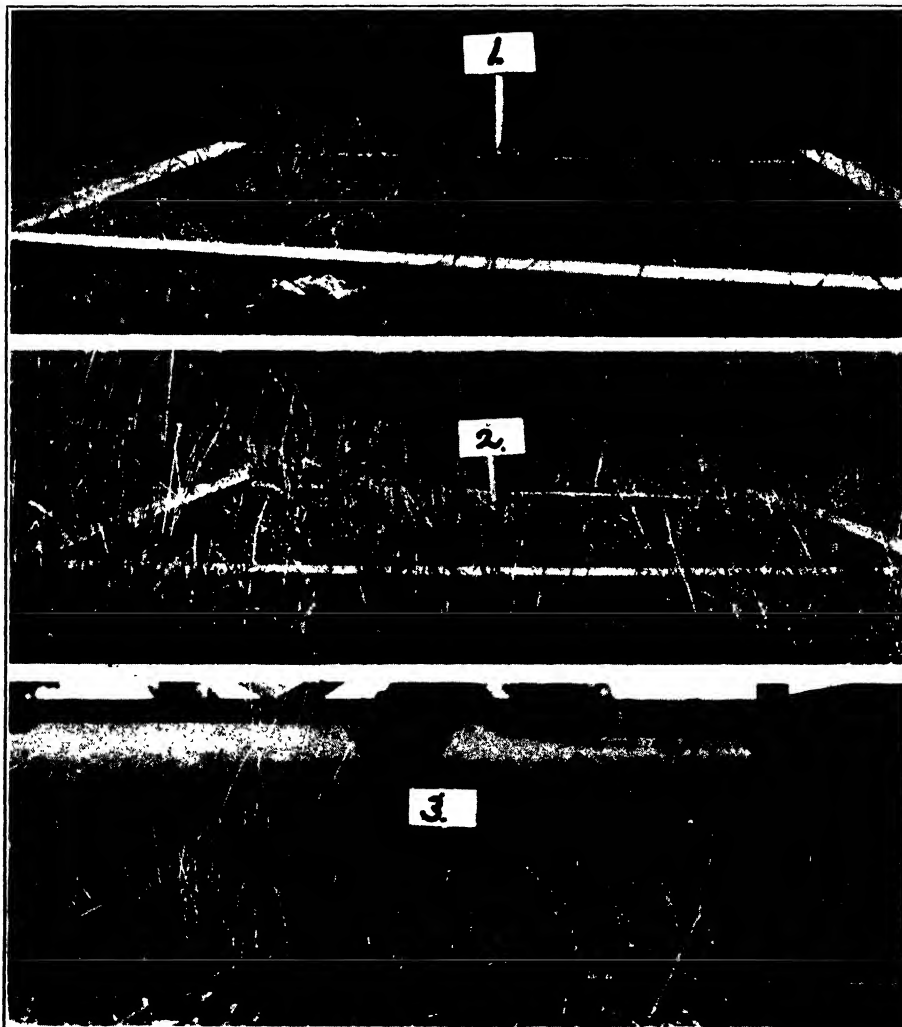


FIG. 31. Quadrat at the McIntyre station protected 1, 2, and 3 years respectively.

unprotected quadrat (Fig. 30). The ground cover was, however, only 7.8 per cent. The average size of the plant mats was the same and the plant cover had practically the same area in the quadrats inside and outside the enclosure at the end of the first summer (Fig. 31). The number of seed stalks, however, and the yield in dry matter had greatly increased in the latter (Table X).

TABLE X. *Data from grazed and protected quadrats on the McIntyre ranch*

Treatment	No. of plants	Size of mats, etc. sq. cm.	Percentage of cover	No. seed stalks	Yield, dry matter, gr.	Per cent increase in yield
Unprotected	216	.31	7.8	72	15	0
Protected 1 yr.	284	.31	8.8	124	41	173
Protected 2 yrs.	192	.79	15.2	218	60	300
Protected 3 yrs.					125	733

The end of the second summer showed again a reduction in the number of plants but the mats had increased nearly 2.6 times in size. The plant cover was about doubled, and seed stalks increased 203 per cent in number. Figure 32 shows a typical quadrat after it had been protected one and two years respectively.

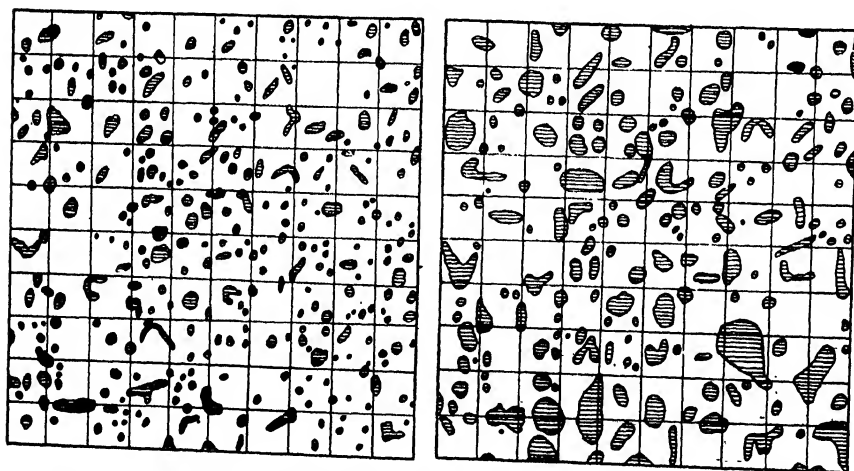


FIG. 32. A quadrat at the McIntyre station protected one (left) and two years respectively. The percentage of ground cover increased from 8.8 to over 15, due to the vigorous growth and fusion of the small clumps of the short grasses into large ones.

KOKERNOTT SPRINGS

Vegetation

The short-grass cover on the mesa at the Kokernott Springs station shows a far greater degree of deterioration than that of either of the preceding stations. The vegetation does not cover more than 1 to 3 per cent of the soil

(Fig. 33). Due to long and intensive overgrazing and trampling, many of the small mats of the grama grasses are dead or are represented only by fragments. *Bouteloua eriopoda* is much in evidence, being both more plentiful and more widely distributed than on the Mitchell flat, a fact that may be due in part to the low water content of the surface adobe soil. None of the grama

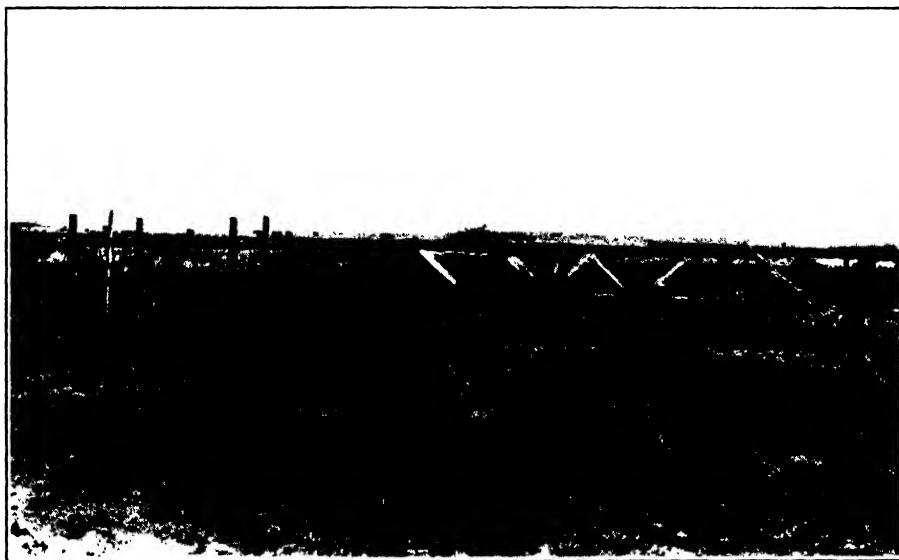


FIG. 33. Detailed view of the sparse vegetation at Kokernott Springs station. The short grasses occupy only 1 to 3 per cent of the surface of the soil.

grasses flower or seed abundantly, so greatly have they been weakened by excessive grazing. In fact, to a large degree, they have been replaced by the rather unpalatable *Scleropogon brevifolius* which, under present conditions, is rapidly increasing its territory.

This grass is more xeric than the gramas, producing an abundance of seeds and flower stalks during extremely dry weather. It is eaten only when young, and the mature leaves and flower stalks, which reach a height of about 6 inches, remain practically untouched while the grama grasses are eaten to the bare ground. *Scleropogon* also propagates vegetatively both by short runners and rhizomes. Very shallow, widely spreading roots enable it to thrive when only the surface inch of soil is moistened.

Owing to the reduction of the grasses in number and vigor, societies are much more numerous than on the Mitchell or McIntyre areas. The only shrubby species is *Condalia spathulata*, which occurs as widely scattered bushes, and an occasional cat's claw (*Acacia*). The following herbaceous species form more or less extensive societies among which the legumes and composites are especially well represented:

Acacia filicioides
Allionia albida
Argemone platyceras
Asclepiodora decumbens
Asclepias brachystephana
Asclepias verticillata
Asclepias arenaria
Astragalus mollissimus
Berlandiera lyrata
Buddleia scordioides
Carduus sp.
Centaurea americana
Clematis drummondii
Condalia spathulata
Convolvulus arvensis
Croton corymbulosus
Dolicholus texanus
Engelmannia pinnatifida

Ephedra trifurca
Eriogonum wrightii
Eriogonum tenellum
Fallugia paradoxa
Gaura coccinea
Gutierrezia texana
Iva dealbata
Mimosa sp.
Opuntia sp.
Perezia nana
Prosopis glandulosa
Ratibida columnifera
Salsola pestifer
Solanum elaeagnifolium
Sophora sericea
Talinum aurantiacum
Vernonia marginata



FIG. 34. A thicket of cat's claw (*Acacia* spp.) too dense for stock to enter.
 Note the excellent development of the grasses.

On certain slightly lower areas where the fertile soil is probably better watered, several species of *Acacia* grow in dense stands. These areas, although local, often cover several square miles. The thorny shrubs reach a height of 5 to 6 feet. Where there is room for symmetrical development the

bushes are 4 to 5 feet in diameter. There seems to be insufficient water for dense stands, and cattle follow paths among the bushes to graze the luxuriant grasses, feed upon the fruits of these leguminous shrubs, and find protection from wind in winter. However, many places are too dense and the thorns are so formidable that the grasses remain uneaten (Fig. 34).

Mesophytic vegetation occurs in an area about a half mile long and an eighth mile wide where running water from perennial springs furnishes a never failing supply (Fig. 13). *Populus wislizeni* and *Salix nigra* with a few *Populus nigra italica* constitute the tree flora. There are no shrubs. The following species of herbs, which with rare exception are not found in the surrounding drier areas, occur here:

Aster salicifolius

Baccharis glutinosa

Datura quercifolia

Helianthus annuus

Leptilon canadense

Mentzelia nuda

Ratibida columnifera

Rumex mexicanus

Scenecio filifolius

Solanum rostratum

Sonchus asper

Xanthium echinatum

Xanthium spinosum

In the water of the springs and the narrow stream that flows from them, a hydrophytic flora is found. This includes species of such genera as *Eleocharis*, *Carex*, *Radicola*, *Mimulus*, *Polygonum*, *Ruppia*, etc., liverworts such as *Riccia*, and numerous algae (*Oscillatoria*, *Hydrodictyon*, *Spirogyra*, *Cladophora*, *Oedogonium*, *Vaucheria*) including the herb-like *Chara*.

Environment

A study of the soil profile, which is often revealed to a depth of 15 to 20 feet in the vertical banks of arroyos, clearly indicates that the area was once the site of swiftly flowing water (Fig. 7). The rounded boulders and enormous beds of gravel deposited by the water have since been covered to depths of 1½ to 3 feet by very fine soil materials. Mechanical analysis of the surface foot (Table XI) shows that the soil consists of one-third clay, and about one-fourth each of silt and very fine sand. There is only 7 per cent coarse gravel.

TABLE XI. Mechanical analysis of soil from the Kokernott Springs station

Fine gravel	Coarse sand	Medium sand	Fine sand	Very fine sand	Silt	Clay
1.0	2.0	2.0	8.8	25.8	27.0	33.4

Thus the porous subsoil is overlaid with a surface soil into which water can penetrate only slowly. It has, however, a high water-holding capacity and is of sufficient depth so that little moisture penetrates into the coarse

subsoil. Roots seldom extend beyond a depth of $2\frac{1}{2}$ to 3 feet. Lime content in this fertile soil is low, being only about 1 per cent in the second and third foot. Here again the soil is neutral in reaction. The hygroscopic coefficient of the surface 6 inches is 9.5; those of the 12 and 18 inch levels are 12.3 and 10.3 respectively. The water-holding capacity in the same sequence is 59, 66, and 68 per cent.

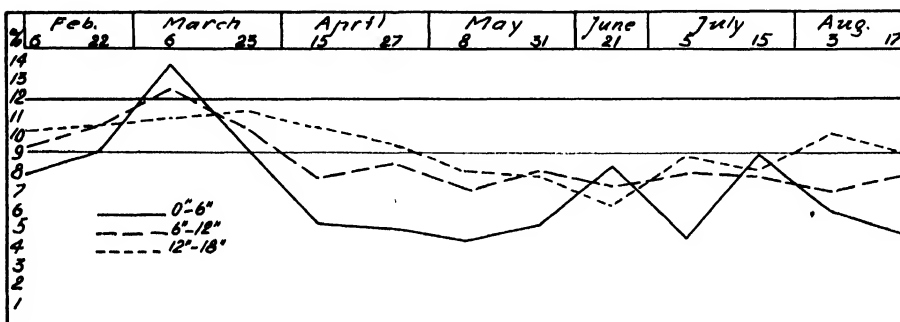


FIG. 35. Water content at the Kokernott Springs station, 1927.

Owing to the compact nature of this fine-textured soil, run-off is high and water content correspondingly low. Determinations of water content were made as at the preceding stations. Figure 35 shows that after the end of March, 1927, the water content in both the first and second 6-inch layers of soil was continuously below the hygroscopic coefficient. At only one time, from February to August, was the water content in excess of the hygroscopic coefficient at the 12 to 18 inch soil level. It seems certain, however, that local

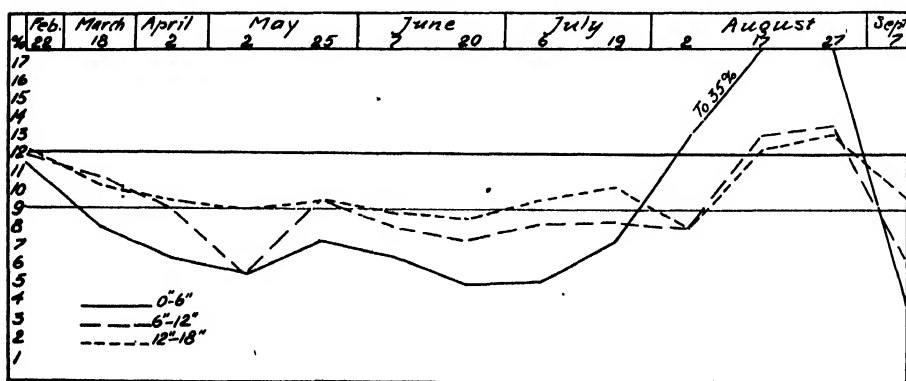


FIG. 36. Water content at the Kokernott Springs station, 1928.

showers between the rather wide dates of sampling furnished water for growth at least during short intervals. The prevalence of drought during the early part of the summer of 1928, and the abundant supply of water during August,

are shown in figure 36. In 1929, water was available for growth both in early spring and late summer, but the usual xeric conditions are also clear (Fig. 37).

Soil temperatures were obtained at the usual depths as shown in Table XII.

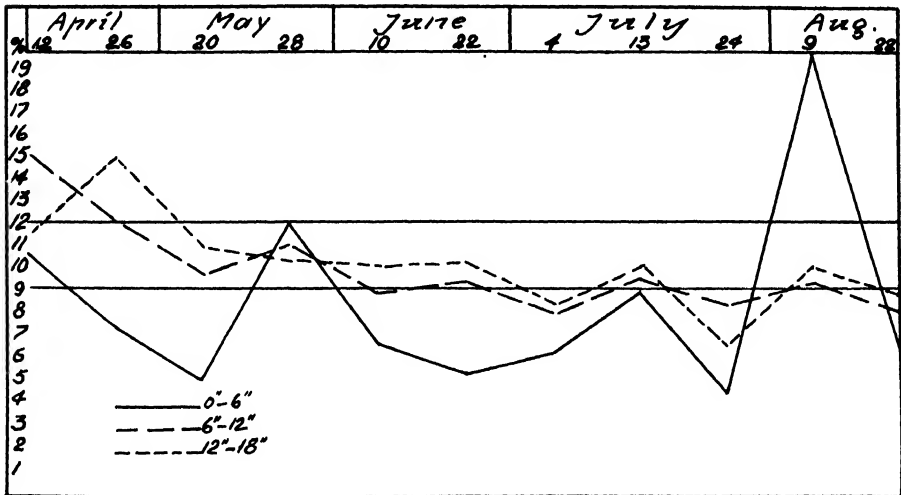


FIG. 37. Water content at the Kokernott Springs station, 1929.

The temperatures of both the surface and deeper soil in January and February were not so low as to prevent root activity. The usual high summer temperatures prevailed in both surface and deeper soil but they were not quite so high here as on the Mitchell flat. Such high surface temperatures would promote great water loss by direct evaporation. Whether or not they are detrimental to root activity of the native species remains to be determined.

TABLE XII. Soil temperature in degrees Fahrenheit at Kokernott Springs

Date, 1927	At 2 in.	At 12 in.	Date, 1928	At 2 in.	At 12 in.	Date, 1929	At 2 in.	At 12 in.
Jan. 19.....	60	54	Feb. 22.....	66	54	Apr. 19.....	82	64
Feb. 11.....	64	56	Mar. 18.....	72	60	Apr. 26.....	90	70
Feb. 22.....	67	60	Apr. 2.....	88	70	May 10.....	110	78
Mar. 11.....	60	56	May 2.....	90	72	May 26.....	68	70
Mar. 23.....	70	58	May 25.....	86	74	June 10.....	94	78
Apr. 15.....	84	66	June 7.....	90	78	June 22.....	100	82
Apr. 27.....	94	76	June 20.....	100	84	July 4.....	108	86
May 8.....	92	78	July 6.....	114	88	July 13.....	100	86
May 31.....	104	86	July 19.....	92	82	July 24.....	100	86
June 21.....	86	80	Aug. 2.....	82	78	Aug. 9.....	76	82
July 5.....	104	84	Aug. 17.....	76	76	Aug. 22.....	96	84
July 15.....	100	86	Aug. 29.....	98	80			
Aug. 3.....	104	88	Sept. 17.....	92	80			
Aug. 18.....	97	86						

A continuous record of evaporation during 1928 shows that extremely high rates (53 to 80 cc.) prevailed during May and June (Table XIII).

TABLE XIII. *Average daily evaporation, from Livingston's cylindrical atmometers, at Kokernott Springs*

1928	Loss in cc.	1929	Loss in cc.
May 25 to June 7	75	Apr. 26 to May 10	87
June 7 to June 20	80	May 10 to May 23	78
June 20 to July 2	53	July 4 to July 13	81
July 2 to July 6	41	July 13 to July 24	48
July 6 to July 19	31	July 24 to Aug. 22	27
July 19 to Aug. 2	17	Aug. 22 to Sept. 2	23
Aug. 2 to Aug. 17	12		
Aug. 17 to Aug. 29	14		
Aug. 29 to Sept. 17	15		

Losses were about half as great during the first 20 days of July, after which they were only 12 to 17 cc. daily during the rainy season until mid-September. This illustrates the wide range of evaporation stress to which the vegetation is subjected during a single growing season. During 1929, evaporation exceeded 77 cc. daily from April 26 until the middle of July, after which the average daily loss decreased from 48 to 23 cc.

Root Distribution

Root studies at this station were limited to an examination of *Bouteloua gracilis*, *Scleropogon brevifolius*, and *Echinocactus horizonthalonius*.

The root habit of the blue grama was very similar to that already described at the McIntyre station. The maximum penetration of living roots was to a depth of 36 inches; a few dead ones were found deeper. Where dry soil was encountered at this level, the root-ends coiled into small tangled mats. The lateral spread was not as great as on the Mitchell flat where the moist soil was shallower. But here again the greatest degree of branching was observed in the surface foot of soil.

Scleropogon has tough, wiry, fibrous roots, about 1 mm. in diameter. The root system consists of two more or less distinct parts, viz., a vertically penetrating, deeper portion and a superficial one. Roots of the former are most abundant and longest, reaching maximum depths of 3 feet. They are fairly well branched throughout, but especially so in the first foot of soil. Horizontal roots extend 18 to 20 inches from the base of the plant, often in the surface 6 inches and not infrequently just below the surface half inch of soil. They are profusely branched with laterals $\frac{1}{4}$ to $\frac{1}{2}$ inch in length and 15 to 20 per inch of main root. The longer ones have branches of the third order. This grass is thus well fitted for absorbing from the surface as well as from the deeper layers of soil. The stolons also early develop both types of roots.

The root system of the spherical *Echinocactus horizonthalonius* likewise

has two parts. The plant excavated had a stem 6 inches in diameter and the vertical root system penetrated 12 inches deep. These fleshy roots were $\frac{1}{4}$ to $\frac{1}{2}$ inch in diameter near their origin, but they soon divided into numerous, much branched, small laterals. These ended in branch-like mats of rootlets. The four horizontal roots ran just beneath the surface of the soil to distances of 3 to 5 feet and none of their branches were over 10 inches deep. Some were very near the surface. They branched abundantly, the laterals being 6 to 12 inches long. They ended by dividing into a great network of absorbing root-ends.

These observations show that the plants at this station depend mainly upon the surface soil for their supply of water, but that the grasses are equipped to absorb water from the deeper soil, as well, whenever it is available.

Studies in Overgrazing

The very sparse vegetation at the Kokernott Springs station is shown in figure 38. Only isolated tufts of the grama grasses remain intact, and the ground cover is scarcely 3 per cent. When cattle are kept out, the remnants

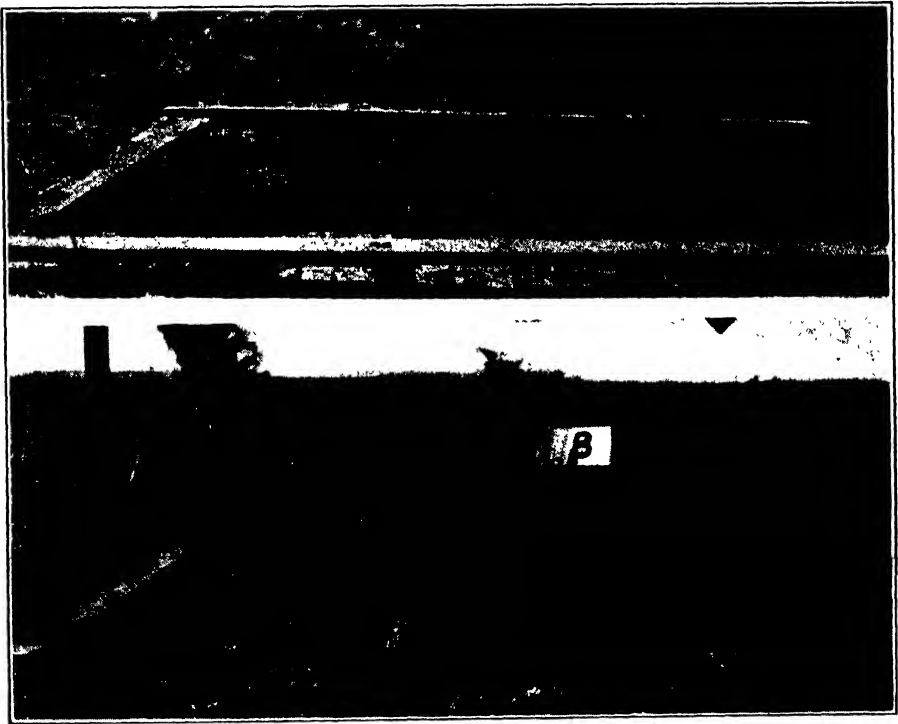


FIG. 38. A. Typical quadrat on the open range at the Kokernott Springs station. The only species present are *Bouteloua gracilis*, *B. hirsuta*, and *Croton corymbulosus*. B. A similar quadrat after three years of protection.

of the vegetation make a weak growth which becomes more accelerated the second year as food is again stored in the starved roots. By the third summer, a really wonderful change takes place, and both flower stalks and seeds are abundantly produced.

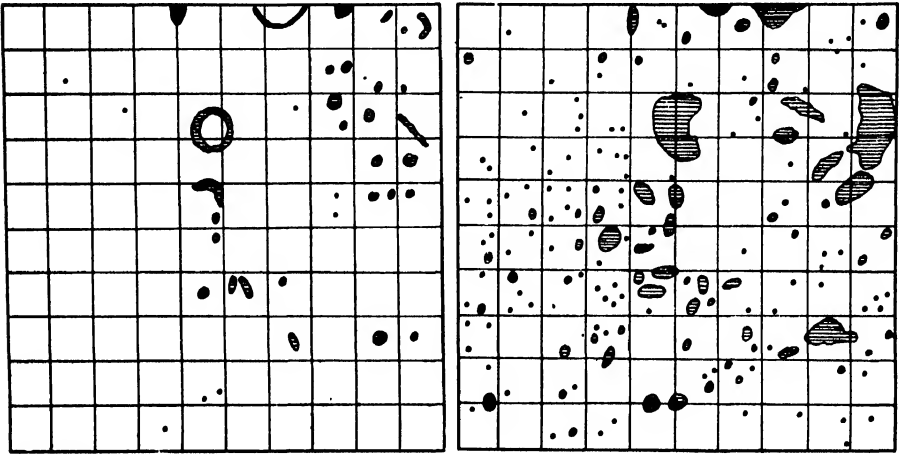


FIG. 39. Quadrats from the Kokernott Springs station protected one (left) and two years. The dots represent annuals, chiefly *Boebera papposa* and species of *Gutierrezia*, and the hatched areas the short grama grasses.

A study of the quadrats (Fig. 39) shows that there is a marked increase in the area occupied by the short grasses, and that annuals are very abundant. The usual data are summarized in Table XIV, where perhaps the most outstanding fact is the enormous increase in forage production.

TABLE XIV. Data from grazed and protected quadrats at Kokernott Springs

Treatment	No. of plants	Size of mats, etc. sq. cm.	Percent-age of cover	No seed stalks	Yield dry matter, gr.	Per cent increase in yield
Unprotected	22	1.2	2.6	108	13	0
Protected 1 yr.	29	1.48	1.4	187	13	0
Protected 2 yrs.	65	.94	6.1	320	32	146
Protected 3 yrs.					131	908

How this range would appear under continued protection or only moderate grazing remains to be determined, but it is certainly clear that it is now so badly deteriorated that the annual forage crop is only a small fraction of the possible yield.

JACKSON-HARMON STATION
Vegetation

The vegetation in the ancient lake bed differs from that at any of the preceding stations. This is due to the much higher water content of the clay soil

which receives considerable run-off water from the surrounding uplands. *Bouteloua hirsuta* and *B. eriopoda* are practically absent, and *B. gracilis* occurs only sparingly. The dominant throughout is tobosa grass (*Hilaria mutica*).

This coarse, wiry grass forms mat-like bunches usually 6 to 12 inches in diameter. The leafy stems reach a height of 8 to 10 inches, and the flower stalks are 4 or 5 inches taller. The grass forms a bushy mat which extends considerably beyond its base, so that the vegetation appears fairly thick although the basal cover is only 10–15 per cent (Fig. 40). It develops rather

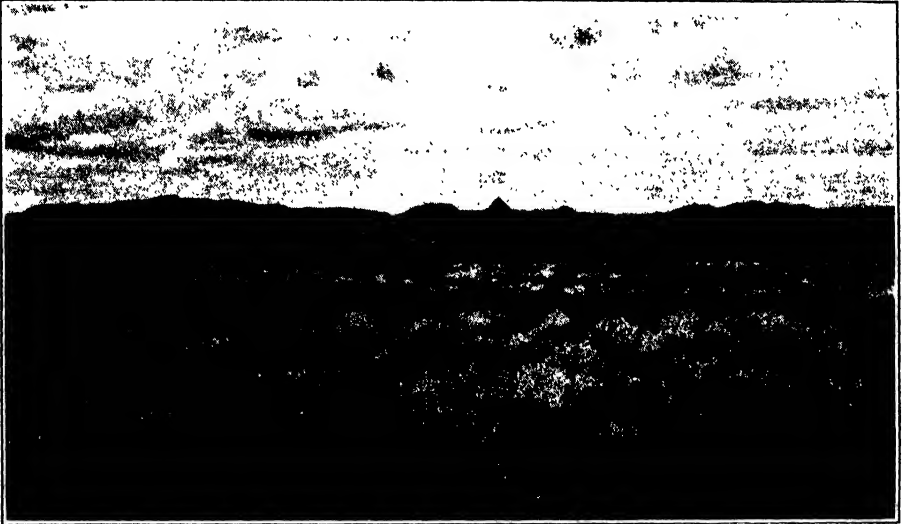


FIG. 40. General view at the Jackson-Harmon ranch. The coarse grass in the foreground is *Hilaria mutica*.

rapidly when water is available, and becomes dry during drought. Upon the advent of rain, the old, apparently dead stems renew growth at the nodes. Its propagation by means of stolons gives it a distinct advantage over nearly all of the other grasses, both as to increasing its area and in resisting the effects of overgrazing. *Hilaria* is not only taller than the short grasses but its roots penetrate much deeper into the clay soil, often to depths of 4 to 5 feet. It furnishes good forage when green but, unlike the gramas, it is not eaten after the foliage dries. Areas dominated by this species are locally known as tobosa flats (cf. Aldous and Shantz, '24).

In local areas where the soil contains a considerable admixture of pebbles, isolated clumps or well developed societies of *Flourensia cernua* are found. This shrub is conspicuous since it overtops the grasses, reaching a height of about 2 feet. It is never denser than that illustrated in figure 41, and its distribution is localized to the well watered soils of the former lake basin. It is nonpalatable to stock.

Other conspicuous societies, especially where the grasses have been closely

grazed, are formed by the matchweed, species of *Gutierrezia*. *G. texana* and *G. divaricata* are somewhat woody annuals. These weedy plants are 1.5 to



FIG. 41. *Flourensia cernua* in a greatly overgrazed area on the Jackson-Harmon ranch. 2' feet tall. They may occur only as scattered individuals among the grasses over the general area, but dense local societies are not infrequent (Fig. 42).

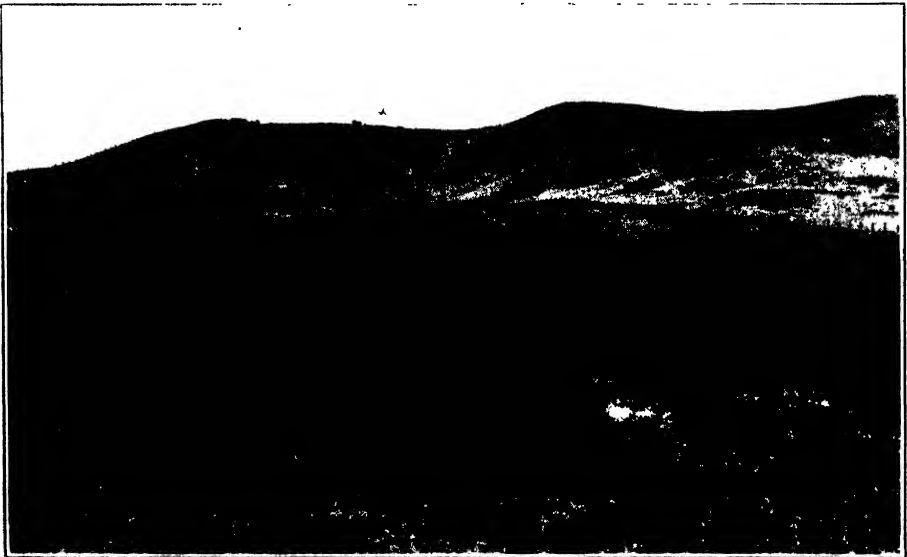


FIG. 42. A dense stand of *Gutierrezia* which is worthless for grazing, a fact which partly accounts for its invasion into overgrazed areas.

They are not grazed and consequently thrive on the excess water when the grasses are closely cropped.

Shrubs of rather rare occurrence are *Prosopis glandulosa*, *Condalia spathulata*, *Odostemon trifoliata*, and *Opuntia arborescens*.

Herbaceous societies in general are not well developed, the following species being the most important:

<i>Argemone intermedia</i>	<i>Machaeranthera tanacetifolia</i>
<i>Astragalus mollissimus</i>	<i>Opuntia</i> sp.
<i>Carduus</i> sp.	<i>Panicum obtusum</i>
<i>Clematis drummondii</i>	<i>Ratibida columnifera</i>
<i>Eupatorium dissectum</i>	<i>Senecio filifolius</i>
<i>Gilia rigida</i>	<i>Sphaeralcea cuspidata</i>
<i>Helenium microcephalum</i>	<i>Tetraneuris linearifolia</i>
<i>Krameria glandulosa</i>	<i>Yucca</i> sp.

Environment

The soil, no doubt, came from the fine materials washed in from the surrounding mountains during the geological past. It is black in color, very sticky when wet, but hard when dry. Indeed, the colloidal content is so high that samples dried in an oven can be broken only with difficulty even with a hammer.

An analysis of the surface foot of soil (Table XV) shows that it consists of more than one-half clay, nearly one-fourth silt, and approximately one-fifth very fine sand. There was only 3 to 4 per cent gravel. Thus, although water can enter but slowly, yet the soil will hold large amounts.

TABLE XV. *Physical analysis of soil from the Jackson-Harmon station*

Fine gravel	Coarse sand	Medium sand	Fine sand	Very fine sand	Silt	Clay
0.6	1.1	0.7	2.8	18.7	24.0	52.1

The texture of the second foot of soil is very similar to the first. At greater depths the soil becomes light yellow in color and possesses a high clay content. At depths of 3.5 to 4.5 feet a calcareous layer occurs which, during dry years, is very compact. When moist, it becomes soft and roots penetrate with ease. The calcium carbonate content of the second, third, and fourth foot respectively is 16.7, 20.9, and 39.2 per cent.

Owing to the fine texture, the hygroscopic coefficients are high. That of the first foot is 16.8, the second 17.5, and the third 18.3. In the fourth foot it is slightly less, 15.0. The maximum water-holding capacity is correspondingly high. For the 6, 12, and 18 inch soil layers it is 67, 72, and 70 per cent respectively.

It is clearly shown that soil moisture conditions were much more favorable for plant growth than at any of the other stations (Fig. 43). During 1927, the water content was high during both spring and fall. There was a period

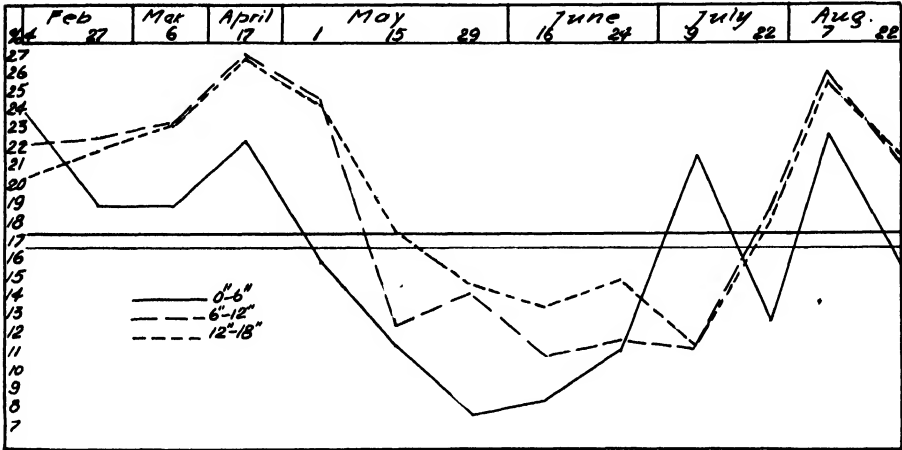


FIG. 43. Water content at the Jackson-Harmon station during 1927.

of early summer drought, however, when no water was available in the surface 18 inches. During this time the tobosa grass became dry, showing that its roots were not securing an adequate supply from the deeper soils.

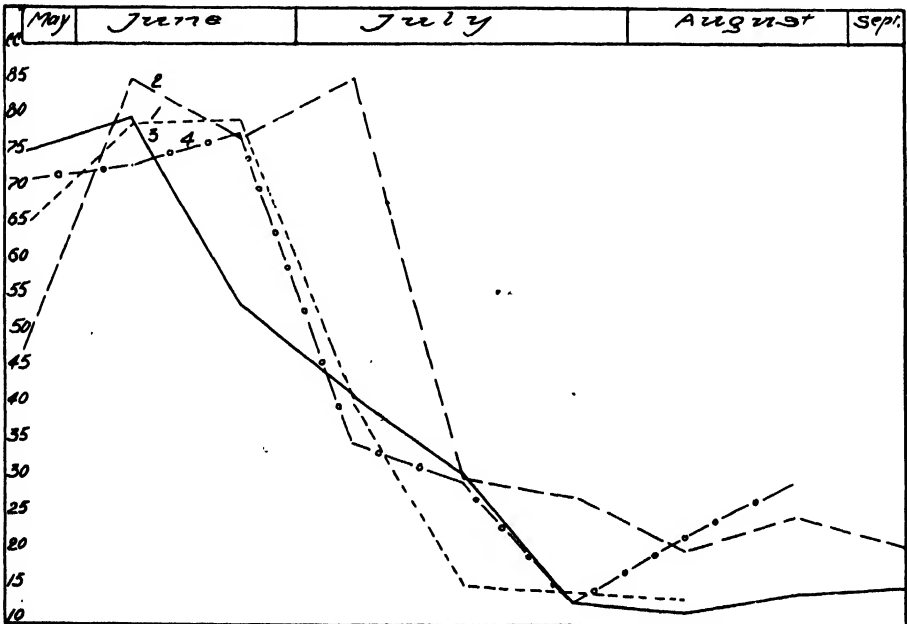


FIG. 44. Average daily evaporation at the several stations during 1928: 1, Mitchell flat; 2, McIntyre station; 3, Kokernott Springs; 4, Jackson-Harmon station.

During 1928, conditions for growth were much more favorable. The water content at all depths usually varied from 20 to 35 per cent, and at only two periods during the season (April and July) was there a deficiency. The following year, a long period of drought occurred between May 15 and August 7; otherwise water was available in considerable amounts. Comparison of available water content with that at any of the preceding stations shows, however, that vegetation here has both the greatest and most constant supply.

Soil temperatures, especially at the 12-inch level, were rather consistently lower than at any of the preceding stations. This was due in the main to the more constant supply of water, which increased the specific heat of this heavy clay soil, but in part to the protecting cover of vegetation which decreased the insolation.

A comparison of the average daily rates of evaporation during 1928, at this and the preceding stations, is shown in figure 44. The most striking feature of these graphs is their general similarity. Unfortunately the stations were too widely separated to permit of simultaneous readings. Some apparent irregularities are due to this, but perhaps the greater ones to local precipitations at the several stations.

Root Distribution

Blue grama grass was again examined, as were also the tobosa grass, a species of *Gutierrezia*, and one of *Flourensia*.

Bouteloua gracilis penetrated deeply, and the lateral spread was only moderate. Many roots reached the 3-foot level where they often ran horizontally a few inches above the layer of high lime content. Branching was profuse throughout.

The fibrous roots of *Hilaria mutica* are very coarse in comparison with the grama grasses, averaging about 1.5 mm. in diameter. They do not spread widely in the surface soil but penetrate deeply. Their course is either vertically downward or obliquely outward and downward at an angle not to exceed 45°. Thus the lateral spread was not more than 22 inches. Many reached the working level at about 3.5 feet, and a few penetrated 5 feet. Branches were not numerous, only 2 to 3 per inch, and they were only 1 to 1.5 inches in length. That the absorbing system was efficient, however, was indicated by the degree of branching which was usually to the third order.

Flourensia cernua is a common shrub where the hold of the grasses has been weakened by constant overgrazing. A single mature plant about 18 inches tall was excavated. The roots are coarse, woody, and superficial; most of them occurred in the surface 6 inches of soil. A few roots penetrated rather straight downward to a maximum depth of 26 inches. The 6 remaining ones spread widely somewhat parallel to the soil surface and in the surface 6 inches. Some were 6 feet long, others 8, and the largest, which was $\frac{3}{4}$ inch in diameter, extended laterally to a distance of 10 feet. One ran outward 4 feet and then turned abruptly downward ending at a depth of 2 feet.

Branching was not profuse. The main branches varied from 4 to 24 inches in length and were very poorly supplied with laterals.

Gutierrezia divaricata was examined because of its importance as an indicator of overgrazing. The plants were 18 inches tall and beginning to blossom. This species has a strong taproot which reached depths of 2 to 2.5 feet. It is well supplied throughout with branches, but the largest and longest originate in the surface 6 inches of soil. These spread almost horizontally, some in the first inch or two, to distances of 1 to 2.2 feet. In addition, hundreds of small rootlets, 5 inches or less in length, thoroughly occupied the soil about the taproot. Branching was extremely profuse throughout. Below 6 inches,

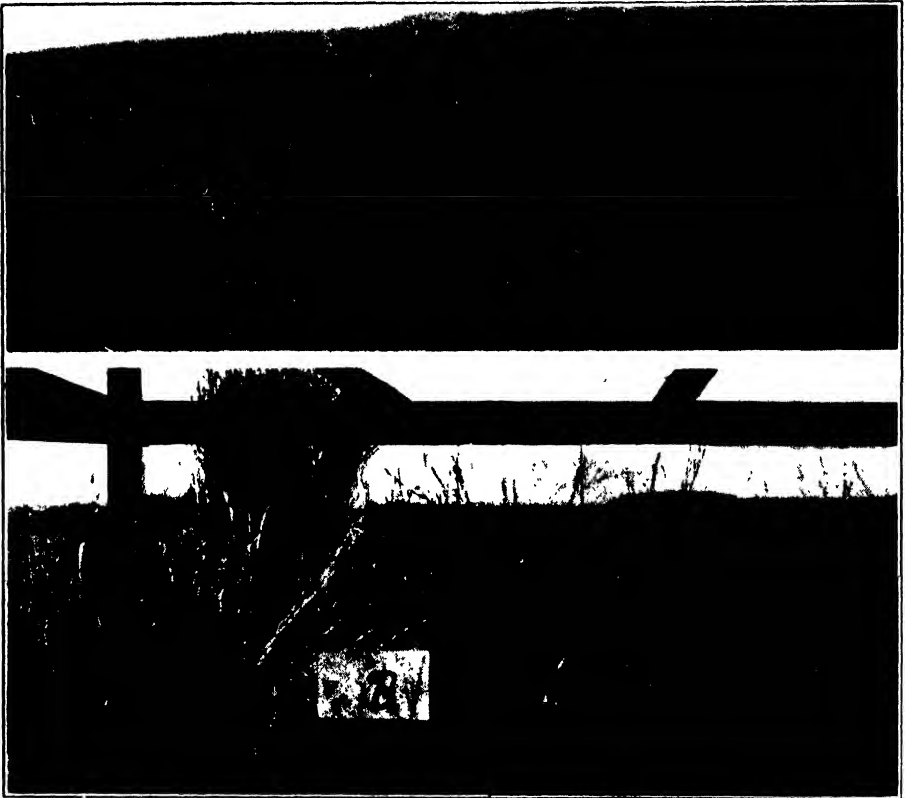


FIG. 45. A, Representative quadrat in the tobosa grass at the Jackson-Harmon station; B, the same after three years of protection.

the branches were fewer and did not exceed 8 inches in length. They decreased gradually both in size and number towards the distal end of the taproot. Secondary and tertiary laterals were abundant but not so profuse as in the surface soil.

These root studies clearly indicate that water penetration is greater in this area which gains an extra supply by the accumulation of run-off water.

Blue grama and the tobosa grass, especially, are well fitted for absorption from the subsoil. *Gutierrezia* likewise penetrated deeply, although it depended mainly, and *Flourensia* almost entirely, upon absorption in the surface soil.

Studies in Overgrazing

A representative quadrat in the unprotected range is shown in figure 45. It may be seen that the cover of *Hilaria* has been grazed back to a height of about 3 inches while *Gutierrezia* remained unharmed. The vegetation, although more abundant than at any of the preceding stations, has a basal cover of only about 8 per cent. After a single year of protection the grasses made a marked growth. This was greatly increased by the end of the second season, and still further gains were made by the third. The chief differences revealed by comparing protected with unprotected quadrats are an increase in the number of plants, a marked gain in the size and number of clumps, and a large increase in the percentage of seedlings. Table XVI shows the gains made by the vegetation under one, two, and three years of protection.

TABLE XVI. *Data from grazed and protected quadrats at the Jackson-Harmon ranch*

Treatment	No. of plants	Size of mats, etc. sq. cm.	Percentage of cover	No. seed stalks	Yield dry matter, gr.	Per cent increase in yield
Unprotected.....	72	1.1	8.0	56	70	
Protected 1 yr.....	41	2.4	9.7	121	184	163
Protected 2 yrs.....	56	2.4	14.2	186	351	400
Protected 3 yrs.....					787	1,024

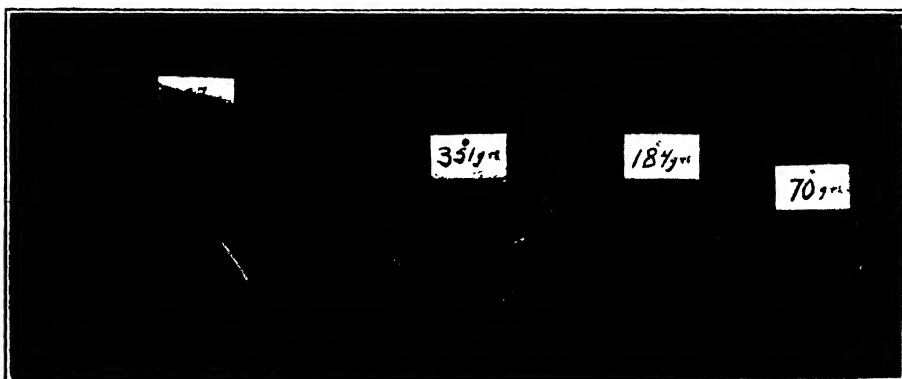


Fig. 46. Average yield of forage in unprotected quadrat (right), and in quadrats protected 1, 2, and 3 years respectively.

The number of plants, the size of the mats and the percentage of cover all show great increases, the last 77.5 per cent. The number of seed stalks more than trebled in two years, and the yield of dry matter increased 1,024 per cent (Fig. 46).

DISCUSSION

The vegetation of this region is a part of the mesquite-grass area (Desert Grassland) described by Shantz ('24), although it is that portion which extends into the mountain valleys and has contact with the coniferous woodland. The invasion of desert scrub and piñon-juniper woodland is in the main a result of the suppression of the grasses and the breaking of the cover of sod by long continued grazing and trampling. Because of the greater size and conspicuousness of the large herbs, shrubs, and trees, greater importance might readily be attributed to them than their control really warrants. Over the area as a whole, xeric grasses are in general possession of the land and if undisturbed utilize almost the total water supply.

This is the southeastern part of the Stockton Plateau described by Bray ('01), who states: "In this [short-grass formation] the great majority of species making up the formation of the eastern prairies [of Texas] have been sifted out by the increasingly arid conditions and only those remain which mark the extreme limit of xerophytic adaptation in grasses." The soil is too arid for agriculture. This has always been and probably always will be primarily a grazing country. Before 1883, the ranges of central and western Texas were free to any one who chose to run stock upon them. Smith ('99) vividly pictures conditions as follows:

"In 1883 the Texas and Pacific Railroad was built through the heart of the range country, and there was an influx both of owners or agents of the lands and of investors who were seeking to acquire free ranges and free grass. Toward the close of this ten-years' shortage of stock there were undoubtedly sections where the native grasses would support 300 head of stock per square mile; and the average carrying capacity of the ranges as a whole was, so far as known, higher than at any time before or since. With the building of the railroad the stock industry underwent a very rapid development. Newcomers who had not seen the land when it was possessed by the Indian, the buffalo and mustang, at the time when the herbage was eaten down, or kept in check by fires or drought, naturally thought that this rich profusion of vegetation was the normal condition and that the saying that it was impossible to put enough cows on the land to eat all the grass was literally true. The result was a rapid and exhausting overstocking of every available square mile of range land. The best grasses were eaten down to their very roots, the roots were trampled into the earth, and every green thing was cut down so that it could neither ripen seed, and thus perpetuate its kind, nor recover from the trampling and exposure of its roots to the air and sun. The recuperative power of the grasses was lessened or destroyed, and weedy species which were present before, but which had been held in check by the luxuriance of the better, dominant sorts, immediately increased in number by rapid bounds. So also the mesquite bean and the cactus, both of which may be destroyed by fire, grew in numbers and commenced to crowd out the grasses."

Aldous and Shantz ('24) state that the normal carrying capacity of the

grama-grass type varies from 20 to 40 head per section. In many places in this Texas area it has been reduced by overgrazing to one-half or even one-third this carrying capacity. Little or no thought is given to the improvement of the vegetation. The privately owned ranges are measured in thousands of acres, grass is grass, and the owners scarcely realize that they may have some part in determining the productivity. When cattle raising is no longer profitable, there is a movement, although not yet of wide-spread extent, to get the rest of the forage with herds of sheep and goats (Fig. 47). Overgrazing has resulted not only in deterioration of the plant cover but also in serious erosion and consequent decreased fertility of the soil.



FIG. 47. Angora goats browsing on the cedars, etc., on a range so greatly overgrazed that it is no longer profitable for the grazing of cattle.

These investigations have shown that, despite the conditions of aridity, protection of the range from stock results in a rapid recovery of the grasses. They extend their area vegetatively, and much bare area is occupied by seedlings. Clipping the vegetation near the end of the summer showed no harmful results, and during the three years of experimentation the average gain in ground cover was 7.5 per cent, and the forage produced increased 795 per cent.

The best method of handling the range is yet to be determined, but from the excellent results obtained by Sampson ('14, '19, '23) it is believed that a combination of deferred and rotation grazing will solve the problem of restoring the range to its maximum productivity. The long growing season and grazing in winter should greatly simplify the problem.

SUMMARY

A study was made of the grassland vegetation of an extensive portion of the Trans-Pecos country in southwestern Texas, with especial reference to grazing.

The region consists of broad flat valleys lying between detached ranges of

low mountains. The altitude of the flats is about 4,000 feet, that of the mountains approximately 7,000.

The soils are variable but usually consist of a silt loam of good water-retaining capacity underlaid at about 2 feet with porous, gravelly subsoil. Deep, less pervious clay soils are found in depressions such as ancient lake beds.

The annual precipitation is 14 inches; most of it falls during July to October. Because of the meager but torrential rainfall the drainage is immature and erosion great. Clear weather with high day and low night temperatures is a characteristic of the climate. Humidity is relatively low and evaporation often extremely high.

The most important factors, water content and evaporation, were measured at four selected stations. No consistent differences were found in the evaporation rates, but the xerophytism of the types of vegetation corresponded in general with the texture and structure of the soil. The less xeric types of vegetation and, in general, the best ground cover occurred on soils with the least run-off and greatest water-holding capacity. The density of the cover, at all stations, however, was profoundly reduced by overgrazing. At three, the xeric cover, chiefly of *Bouteloua gracilis* and *B. hirsuta*, but with *Scleropogon brevifolius* where overgrazing was worst, cured on the ground during intermittent and extended periods of drought, when available water was exhausted to a depth of 2 feet. The subclimax *Hilaria mutica* at the lake-bed station had a much larger and more constant water supply, but it too suffered occasional drought.

Root relations were determined at all stations. In general, absorption was greatest in the surface soil, but occurred throughout the first 2 feet.

Due to overgrazing and breaking of the grass cover, various elements of the xeric woodland, and especially of the desert scrub, are extending into the grassland.

Quadrat studies at 4 selected stations showed that the ground cover varied from 1.2 to 8 per cent. A single year of protection increased it to an average of 7.5 per cent, and 3 years of protection to 12 per cent. Forage production was increased 862 per cent by 3 years of protection, when the forage was removed in the fall. Methods of restoring the range to maximum production are suggested.

This work was done on the suggestion of Prof. J. E. Weaver to whom the writer is deeply indebted for efficient direction.

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VERTICAL OSCILLATIONS OR SEICHES IN LAKES AS A FACTOR IN THE AQUATIC ENVIRONMENT¹

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DEFINITION AND OCCURRENCE OF SEICHES

The oscillatory movements, termed seiches, which occur in lakes throughout the world, have long been known to limnologists and others interested in the problems of lakes; but since these movements have been studied primarily from the standpoint of the physicist, their ecological bearings have not been emphasized.

A seiche is, essentially, a vertical oscillation of the water of a lake. Along a given axis the water may oscillate as a single unit, in which case the seiche is a uninodal one, or there may be two or more nodes in the oscillation, thus making a binodal or a multinodal seiche. In any given lake there are usually several axes of oscillation, extending in different directions; therefore several types of seiches differing in amplitude, direction and nodal form may be occurring simultaneously. The general nature of a seiche is represented by the graph in figure 1. To properly interpret it, one must conceive of the surface

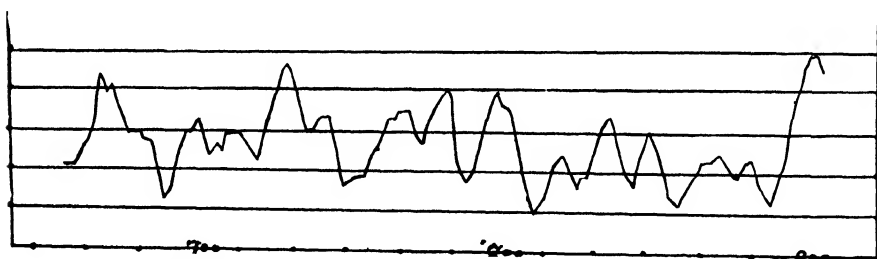


FIG. 1. Graph of seiche oscillations. The graph is based on records obtained from Lake Michigan. In the horizontal row of small circles beneath the graph, each space indicates a time interval of 10 minutes. In the vertical row of circles at the left of the graph, each space represents 1 inch. The figures 7.00, 8.00, 9.00 indicate hours A.M.

of the lake as rising and falling at a given spot, in a continuous series of stationary vertical oscillations of the type indicated by reading the graph from left to right. In the particular series represented there is a major movement, and, superimposed on it, minor movements which represent seiches having a different axis and periodicity.

¹ This work was done while in residence at the Franz Theodore Stone Laboratory, Put-in-Bay, Ohio.

The possible causes of the seiche movement have been discussed by Forel ('95). He was of the opinion that the oscillations are set up by an area of exalted atmospheric pressure bearing down upon a particular region of a lake and pushing the water out to regions of lower pressure. When the exalted pressure passes, the water surges back, and, in the process of gaining a state of equilibrium, exhibits the oscillatory movement of a seiche. Forel's view undoubtedly explains some seiches, perhaps all seiches that occur in lakes protected from winds, but there is evidence (Krecker, '29) that in wind-swept lakes, winds are an important agency in developing the seiche movement.

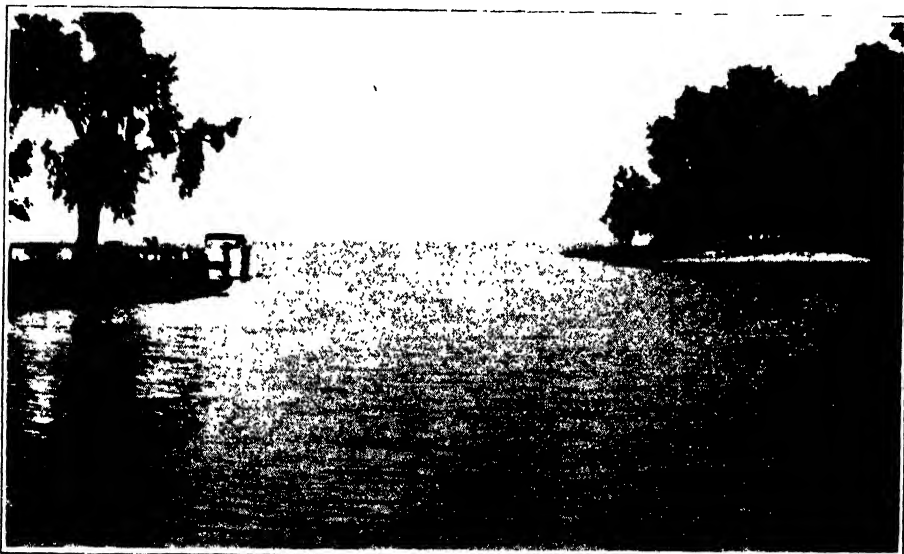


FIG. 2. Entrance channel into a lagoon (East Harbor). The picture was taken from a point at the inner end of the channel and presents the view toward Lake Erie. The outer end of the channel would be marked by a line drawn from the rear of the motor boat to the grassy tip of land on the right. The channel is 15 feet deep and about 100 feet wide.

A recent book by Halbfass ('23) presents a comprehensive review of our knowledge of the subject to date. The most extensive and thorough work has been done on European lakes. Information on seiches in American lakes is rather meager, most of it consisting of isolated instances which attracted attention by reason of their extreme nature. A number of such cases, which occurred in the early years of the country, are mentioned by Whittlesey ('74). Henry ('02) carried out an extended series of observations on the major seiches of Lake Erie, and Krecker ('29)² recently published observations

² The reader is referred to this paper for detailed information regarding a number of facts used as a basis for the present discussion. The paper deals with the purely physical aspects of seiches.

covering certain features of the seiches in the same lake. Since these observations were made, some data on seiches in Lake Michigan have been obtained by the writer.

From an ecological standpoint, seiches are of interest because they are capable of developing conditions that modify the environment of animals and plants in lakes, especially those inhabiting backwaters and shoals.

Along the borders of lakes with low-lying shores there frequently occur marshy backwaters, lagoons or embayments, as they may be variously called, which are separated from the lake proper by bars of one type or another. In Lake Eric, where the observations recorded in this paper, were chiefly made, there are a number of such backwaters. Certain of them differ from the rest in being connected with the lake by channels (Fig. 2) and in having their

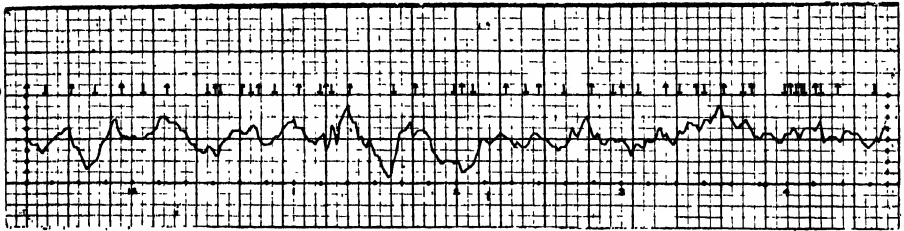


FIG. 3. Graph showing the relation between the seiche oscillations and the currents in a channel connecting a lagoon with Lake Eric. The arrows pointing up mark the start of a current flowing toward the lake, and the arrows pointing down mark the start of a current flowing into the lagoon. The graph represents the oscillations of the seiche. The spaces between the dots arranged in a horizontal row beneath the graph indicate a time interval of ten minutes. The figures indicate hours P.M. The distance between the dots in the vertical row at the left represents $\frac{1}{2}$ inch.

vegetation arranged in definite patches separated by open waterways (Fig. 4).

The water in the channels connecting a lagoon with a lake is constantly moving to and fro as a definite current. This current is directly due to the action of the seiche movement, as reference to figure 3 will show. With the upward swing of the oscillation the current sweeps in, and with the downward swing it flows out. The rate of flow varies with the height of the oscillation. Sometimes it is barely visible, and again it moves with considerable strength. The most rapid movement recorded was 2.5 feet per second. These reversing currents maintain the channels, aided by the scouring action of huge blocks of ice during the winter, and by the favorable location of the backwaters. A favorable location appears to be one in which a curve in the shore line or an outlying shoal prevents the channel from being closed by the wash of a violent storm.

A variety of observable intermediate conditions indicate that the channels through the bars represent the culmination of a sequence of events about as follows. The enclosed areas with which the channels connect were originally broadly connected with the lake and became detached by the growth of an

intervening bar. While the embayments were broadly connected the movements of the seiche merely altered the water level; as the connection became narrower evidences of a current developed and eventually a point was reached when the current was sufficiently strong to prevent any further closing, or, at least, to so delay the process as to give a degree of semi-permanence to the channel.

SEICHE-CURRENTS AND VEGETATION

Within the backwaters the currents are responsible for open pathways of water that divide the vegetation into definite patches. The exact arrangement of the patches depends upon local conditions. Where the channel through the bar is relatively short and wide, so that the current does not lose strength by reason of a long channel, the intruding water keeps a certain area, which might be termed the entrance pool, entirely free of vegetation. If the backwater is small there may be no other noticeable effect on the plants. In a large embayment several channels may radiate from the entrance pool and wind through the vegetation for two-thirds of a mile or more, occasionally subdividing as they go (Fig. 4). Where the entrance channel is long, or where other conditions occur, there may be no entrance pool but merely one or more channels through the vegetation.

Where the currents are strongest there is a sharp alignment of dense vegetation along the channels, while to the rear or beyond the effective strength of the current, the vegetation frays out irregularly. In a well developed channel there may be found a definite zonation of the plants, beginning frequently with *Sagittaria* along the edges, followed by various other types such as *Calamus*, *Scirpus americanus* and *Scirpus validus*. This inner zone becomes progressively thinner to the rear and frays out irregularly with *Sagittaria* again appearing abundantly. Beyond the limits of the channels, emergent vegetation is thinly scattered; patches of submerged *Potamogeton* and *Vallisneria* appear irregularly.

The denseness of the vegetation along the channels, especially about the entrance pool, is probably to be explained by the fact that, as the embayments became separated, a line of silt was deposited where the incoming currents met the impounded water. There was thus provided, early in the history of the lagoon, a favorable substratum for rooted vegetation. Once started, the vegetation and further accumulations of silt would combine to maintain this zone in an advanced condition.

SEICHE-CURRENTS AND ANIMALS

The disposition of the vegetation is, of course, the most readily visible influence of the seiche-currents, but equally important is their effect on the animal life of the backwaters. The warm shoal waters of these areas afford extensive spawning-grounds for fish, and provide an abundant food supply in the innumerable forms which find such waters an ideal habitat. From the stand-

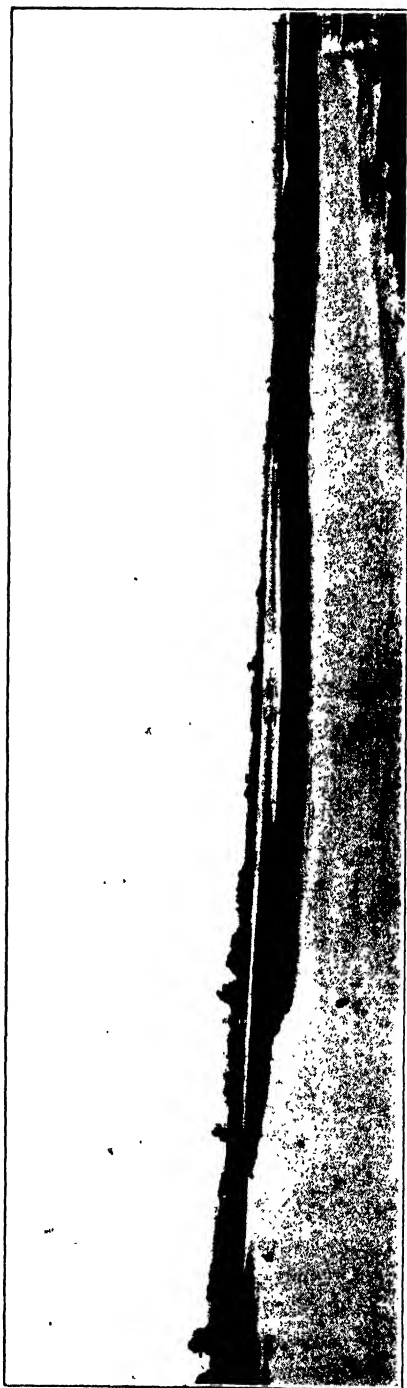


FIG. 4. Channels through vegetation in a lagoon (East Harbor). The picture was taken from a point just inside the main entrance to the lagoon. The view shows two of three main channels maintained by the seiche currents, through the vegetation. The channel on the left is the center one of the three. Its inner end is hidden by a bend to the right. The channel on the right extends beyond the limits of the picture and then turns back so that its inner end can be seen a short distance to left of the right side of the picture. The channel splits just before reaching this point so that a branch extends farther to the left. This branch can be barely traced by a faint light line through the vegetation.

point of the lake as a whole, one of the chief effects of the seiche-currents, in fact probably their most important effect, is that, through the channels which they maintain, they afford indispensable feeding and breeding grounds to thousands of fishes. When the water is clear, fishes can be seen constantly passing to and fro between the lake and the embayments. In so far as fishes suitable for human food enter into consideration, the economic aspects of the situation are of considerable importance. Perch, sunfish, white bass, carp and black bass make use of the lagoons in large numbers.

Other lake-inhabiting forms, to which the seiche-currents make these embayments available, are the snails *Goniobasis livescens* and *Pleurocera elevatum*. Neither of these is normally found in the ponds and marshes which are completely separated from the lake by an unbroken bar. Information available regarding animal distribution within the embayments indicates that the currents exert their influence largely through their direct physical effect. As will be mentioned later, the currents affect temperature, hydrogen ion concentration, etc., but there is no evidence that the variations induced affect the macrofauna. The microscopic forms have not been sufficiently studied to draw conclusions. The currents through the entrance are strong enough to sweep the bottom of the channel clear of all fine sediment, leaving nothing but coarse-gravel. Animals are practically absent. Several dredgings at one of the larger embayments resulted in a single specimen each of the clam *Leptodon fragiles* and the snails *Physa* and *Goniobasis*. A short distance beyond the entrance, fine sand occurred, and here several dredgings produced two snails, both *Campeloma*. About three hundred yards within the embayment, fine mud appears and here several of the clams were obtained, also bloodworms, the leech *Herpobdella punctata* and two specimens of the annelid *Sparganophilus*. At the inner end of the channels there appeared, in addition to the forms already mentioned, parnid beetle larvae, larvae of the mayfly *Hexagenia*, and the snails *Planorbis* and *Amnicola*.

Characteristic animals of the more advanced plant areas are the snails, *Lymnaea humilis*, *Planorbis trivolvis*, *Ancylus rivularis*, *Amnicola limosa*, the leech *Herpobdella punctata*, bloodworms of the midge genus *Chironomus* and the flatworm *Planaria maculata*. Of these forms the most abundant are *Ancylus*, *Amnicola* and the blood worms, especially on the rush-like vegetation. The bloodworms were found inside the stems in a honeycomb of tunnels.

SEICHE-CURRENTS AND PHYSICAL CONDITIONS

Physical conditions such as temperature, hydrogen ion concentration, and transparency are subject to so many local variations, even in an ordinary pond, that seiche influence may be questioned. However, several series of temperature readings show that temperatures at the entrance to the lagoons are 2 to 3 or more degrees C. lower than those at the inner end. Specific instances taken from a small lagoon are: lake 27° C., pond entrance 27°, center of pond 28.5°

center of pond 31° , inner end 31° . A similar example from a larger embayment is: lake 22° C., entrance 23° , inner end of channel 25° , mile beyond the entrance 28° .

Variations in pH appear to be on about the same basis, that is, the nearer the lake, the closer the approximation to lake conditions. Two specific instances from a large embayment are: pH 7.4 in the lake, and a progressive change toward greater alkalinity along the channels up to pH 8.2 some distance beyond their inner end; pH 8.4 at the entrance, and a gradual change to pH 9.2 a mile inside the entrance.

Transparency conditions correspond in a similar manner. The transparency at a small, muddy embayment was frequently as follows: lake 6' 6"; entrance 3' 6"; center 2' 6"; inner end 1' 8". In the larger embayments the water is often clearer than it is in the smaller places. The difference is sometimes so marked that the larger embayment is even clearer than the lake. Since transparency has an important bearing on photosynthesis, it would appear that photosynthetic conditions in the small ponds are most favorable at the entrance, whereas in the larger embayments they are best at some distance inside the entrance, where the effect of the lake waters is lost.

SEICHES AND SHOAL WATER FORMS

More widely felt than seiche currents, which can occur only under certain specific conditions, are the constant fluctuations in water level which the seiches produce along the entire shore of a lake. The fluctuation may not be more than a fraction of an inch in some cases and again it may be 4 or 5 inches. So far as my observations go, the usual fluctuation during the summer months has been about 2 inches in Lake Erie, but a fluctuation of 3 to 4 inches occurs frequently enough to be a factor. Although this is not large, it is sufficient to affect the animals of shoals and reefs. In a low-bordered lake such as Erie there are numerous areas involving, in the aggregate, thousands of square feet where the water is not more than 2 to 3 inches deep for a distance of 15 to 20 feet from shore. Many animals inhabit areas of this sort in large numbers. Among them are insect larvae such as midges, mayflies and caddis flies, snails of the genera *Lymnaea* and *Physa*. At this depth one frequently finds the eggs and young of the snails in vast numbers. For example, in 4 inches of water along the shores of Lake Erie there were found, in one case, within an area 3 feet square, 661 individuals representing 11 different species, and in another instance 1,189 individuals representing 17 species.

The time required to complete a seiche oscillation varies from a few minutes to several hours. A period of 40 minutes is rather common, and accompanying fluctuations of 3 to 4 inches in water level are also frequent. Therefore, on the basis of roughly average conditions, it is not unusual for the water level at any given spot to be lowered 1.5 to 2 inches for a period of 20 minutes.

This means that for a corresponding length of time the forms inhabiting gently sloping shores may either be partly or entirely exposed. The adverse effects of such a situation are not merely an exposure to the air, but also a difference in the amount of exposure to the grinding action of waves. On a gently sloping surface, the effect of mere ripples is greatly magnified and, therefore, a change in the depth of the water, even if only an inch or two, may mean the difference between exposure to wave action and protection from it.

In conclusion it need hardly be said that the foregoing observations do not represent an exhaustive treatment of the subject. The observations have been offered in the hope that seiche phenomena will attract more attention in connection with limnological studies.

SUMMARY

Vertical fixed oscillations, known as seiches, which occur in bodies of fresh water, create currents in favorable situations, and maintain channels which connect lagoons and other semi-detached areas of water with the main body. The currents entering the lagoons influence the distribution of both plants and animals. They also affect such conditions as temperature, pH, and transparency. The connecting channels serve to make the lagoons available to the fish of the region as a feeding and breeding ground. In addition to these results, the seiches maintain a tension zone along the entire shore line of the waters in which they occur. The importance of this is greatest in shoal areas.

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OBSERVATIONS ON THE AFRICAN LUNG-FISH, *PROTOPTERUS ÆTHIOPICUS*, AND ON EVOLUTION FROM WATER TO LAND ENVIRONMENTS

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In the whole course of vertebrate evolution there have been few events so momentous as the emergence from aquatic to terrestrial life. It is now generally recognized that the amphibia were evolved from fresh water fishes, and that fluctuations of climate were the principle driving force underlying this evolution. Though we commonly associate lungs and aerial respiration with the amphibia and higher animals only, it is probable that efficient lungs were evolved long before, and independently of, terrestrial locomotor apparatus. Aerial respiration was an adjunct to branchial respiration in the most ancient teleostome fishes, and persists today in many primitive fishes which lack efficient means of moving about on land.

Among the recent fishes the most interesting air-breathers are the Dipnoi, or lung-fishes. The Dipnoi are a very archaic group, known from the Devonian and doubtless originating in the Silurian. Among the vertebrates they are exceeded in antiquity only by the ostracoderms and the elasmobranchs. Though once widely distributed over Africa, Europe, the East Indies, Australia and America, they are now geographically isolated and reduced to three genera: *Protopterus*, with three species in Equatorial Africa, *Lepidosiren*, with one species in South America, and *Neoceratodus*, with one species in Australia.

The anatomy of the Dipnoi has been carefully studied by several observers but no detailed physiological or biochemical observations on them have ever been recorded. Through the favor of the John Simon Guggenheim Memorial Foundation, it was possible for Dr. James P. Baker and the author to collect a number of specimens of the African Dipnoan, *Protopterus*, and to bring them alive to New York for biochemical study. Some of these fish have been induced to enter into estivation under controlled conditions in the laboratory, and careful metabolic observations have been made upon them in both the active and estivating state. The results of these observations have been published elsewhere (Smith, '30), and it is intended to report here only such observations as are of general biological interest.

It is interesting to note the importance of the Dipnoi from an evolutionary point of view. Aerial respiration was apparently first achieved by ganoid forms higher than the elasmobranchs, but ancestral to the *Crossopterygii* and Dipnoi. Through one branch of the earliest ganoids the primitive lung was

passed on to the lower members of the higher fishes (Actinopterygii) and through the crossop-dipnoan stock to the first terrestrial animals. The evidence for this conclusion is partly direct, in that such forms as the Devonian crossopterygian *Osteolepis* possessed a pair of small, laterally placed olfactory cavities which communicated between the exterior and the buccal cavity, exactly as in the tetrapods. This arrangement, which has no parallel in any other group of fish except imperfectly in the Dipnoi, presumably implies that *Osteolepis* habitually breathed air to reinforce the oxygen which it received through the gills (Watson, '25). In the carboniferous coelacanth, which were descendants of the osteolepids, the air bladder was calcified and is beautifully preserved in fossil specimens (Goodrich, '09). By the Triassic and Cretaceous, the coelacanth nostril had been reduced to simply an external opening as in the higher fishes (Watson, '25).

Indirect evidence that the early Crossopterygii possessed a respiratory air bladder lies in the fact that such an organ is present and constitutes a primitive character in the lower actinopterygian fishes as well as in the Dipnoi which must have shared with the former a common Silurian ancestral group. Furthermore, among the Devonian Crossopterygii, in forms closely related to the earliest known dipnoan, *Dipterus*, lies the fish which is believed to have been ancestral to the first air-breathing, terrestrial animals. There is little evidence to indicate that the respiratory organ has been acquired independently by the dipnoan, actinopterygian and amphibian branches. There is, on the other hand, much evidence in the comparative anatomy of the lungs, heart and circulation to indicate that such is not the case. The assumption is warranted, therefore, that a lung, in the form of an air bladder opening off the ventral surface of the esophagus, was present in the early ganoids before the lines leading to the Dipnoi, the Crossopterygii and the Amphibia had separated from the parent stem.

Important as the primitive lung was for the Devonian fishes, it has, apparently, not been of sufficient value to the recent fishes to be improved upon, or even retained. Except in a few primitive forms such as *Polypterus*,¹ *Amia* and *Lepidosteus* where it is still used as a respiratory organ, it has been diverted to other purposes, such as the swim-bladder, or it has disappeared entirely, as in many of teleost fishes.

In the Dipnoi, on the other hand, the primitive lung persists as such and these fishes, though markedly differentiated in their fins and skull from the ganoid stock which stands as ancestral to the terrestrial vertebrates, continue to lead a life very similar, we may imagine, to that led by the early air-breathing Crossopterygii. *Protopterus*² and *Lepidosiren* use their lungs as the prin-

¹ Histological observations on the blood and tissues of active and estivating fish will be reported by Speidel and Jordan ('30) and the kidneys will be described by MacNeider ('30).

² We have had an opportunity to study living specimens of *Polypterus senegalus* obtained at Packwach, Uganda, one of which was brought to New York alive. We can definitely state that *polypterus* occasionally rises to the surface, gulps air and releases the

cial means of respiration; apart from an apparent inability to get food, they can live almost indefinitely out of water; and when stranded in dessicating mud-flats, they bury themselves in the mud and live without food or water, and with constant aerial respiration, for long periods of time. In attaching historical significance to the life habits of the recent Dipnoi, it is appropriate to quote Noble ('27) who has said in another connection, "On close scrutiny, habits in many of the lower vertebrates may be more stable than many structural characters. There is no way of knowing *a priori* whether habit, and by this I mean instinct, or structure is the more conservative in evolution."

The exact circumstances culminating in the evolution of lungs are not known, but the general features of the climate and habitat obtaining during the period of this evolution have been deduced from the paleontological record. Barrell ('16) has crystallized the view that the chief cause that gave rise to lungs was the nature of the contemporary climate. The late Silurian and early Devonian periods, which comprise the horizons in which air-breathing fishes were first evolved, consisted mainly of inland lake and lagoon deposits formed under arid or semi-arid conditions. The mean temperature in the Silurian era was, perhaps, as much as 23° F. higher than at present, and the northern continental areas had a hot, desert climate whose dry periods were only occasionally interrupted by thundery rains (Brooks, '26). The extensive mountain building which occurred during the Silurian led, no doubt, to widespread drainage of the continental areas and consequently to a reduction in the stable masses of fresh water in which, at this time, the fishes entirely made their home. The marked alternation of wet and dry seasons compelled those fishes which should survive to make larger and larger use of air. Judging from the adaptations which are found among the recent fishes, several methods of aerial respiration may have been tried out; some fishes may have taken air into the mouth, to expel it again by this route; some may have swallowed air and passed it through the intestinal tract; some may have developed accessory respiratory apparatus in the capillary bed of the tail or fins; but it appears that those forms which were destined, for whatever reason, to be the fore-runners of the terrestrial forms, swallowed the air and passed it into a diverticulum of the esophagus, expelling it by the same route. Thus they were able to survive in dessicated pools, and perhaps to enter into estivation until relief from the torrid summer had come.

Accepting Barrell's view we see in the life history of the estivating Dipnoi a recapitulation of one of the most crucial evolutionary periods through which excess air through the gill covers as it sinks again to the bottom. This aerial respiration may occur at 20-minute intervals, although the fish has been observed to lie for over 2 hours without coming to the surface once. *Protopterus* and a specimen of *Lepidosiren* observed at the New York Aquarium showed as much irregularity in aerial respiration. That *Polypterus* has more efficient aquatic respiration is shown by the fact that in this fish branchial respiration occurs uniformly at about 20 to 30 times per minute, while *Protopterus* may show no branchial respiration over a period of hours (see also Harrington, 1899a, b, and Budgett, 1899, 1903).

the higher vertebrates have passed. Though they are excluded by definite morphological characters as the possible ancestors of the terrestrial vertebrates, they arose with these from a common stock, and their mode of life, remaining essentially unchanged since the Devonian, reflects the adaptations which must have been widespread at that time and which were probably shared by the proto-terrestrial forms.

The lung-fish which we have examined are specimens of *Protopterus aethiopicus* Heckel, collected at Kismu on the Eastern shore of Lake Victoria. *Protopterus* is fairly abundant and is the largest fish in Lake Victoria. This species is probably the largest of the lung-fish. There is a specimen in the Kenya Natural History Museum, Nairobi, taken by native fisherman in the Kavirondo Gulf near Kisumu, which is 7 feet long and weighed over 90 pounds.

This fish is called "Kamongo" by the natives of the Kavirondo district; it is also frequently designated by the Swahili terms *samaki ya dongo* meaning "fish of the mud," and *mamba*, which properly means crocodile. It is said by the natives to be a cross between a crocodile and a fish, a concept based no doubt on its dangerous bite and its swampland habits.

Kamongo is relished by the natives as an article of diet. Large numbers of the fish are sold daily in the native markets, and our own boys usually carried our laboratory material to the kitchen when we were through with it. On one occasion we were innocently served with Kamongo by the cook; it is coarse meat, possessing a muddy flavor like that of estuarine flounder. During the dry season the natives follow the watercourses and mud-flats, searching for the burrows of the fish. A stick is thrust into every suspicious hole or mass of papyrus roots; if the end of the stick on withdrawal smells of fish, the victim is disinterred. Sometimes on being disturbed the fish "barks," thus giving itself away.

The African lung-fish, *Protopterus*, was discovered in 1835 (Jardine, 1841) and described by Peters in 1844. It occasioned, as one might suppose, great interest because of its peculiar life habits and its presumed relationship to the Amphibia. Living estivating specimens, dug up with the surrounding mud intact, were transported to England and Germany on several occasions (Jardine, 1841; Macdonnell, 1858; Gray, 1856; Wiedersheim, 1887). Parker (1889, 1890-1891, 1892) obtained 100 specimens in this manner and prepared a detailed anatomical description. All these exported specimens were from the Gambia River, and presumably belonged to the species *P. annectens*.

Several specimens have been shipped from England to the United States in their mud nests. These, as well as many of those sent to Europe, were subsequently removed from the mud and kept in aquaria where they survived for considerable periods (Dean, '06, '12a, b).

The only descriptions of the estivating habits of *Protopterus* which have been published concern the Gambian species, *annectens*. We were unable to

obtain any estivating specimens of *P. aethiopicus*, though we have observed them pass into estivation under laboratory conditions. What information we could gather indicates that the estivating habits of the two species are similar. During the dry season, those individuals which are stranded in dessicating areas by the recession of the waters bury themselves in the mud where they become encased in a cocoon, in which they remain until that area is again covered with water. When dug out of the dried mud, the fish is found curled in a chamber communicating with the exterior by a passage through which the fish gets air. The burrow may be from 12 to 18 inches underground.

The fish is closely covered by a cocoon which was stated by earlier observers to be made of dried leaves, but was later shown to consist of the dried mucous secretions given off by glands in the skin of the animal. This cocoon entirely envelops the fish except for a small opening which leads into the mouth (Jardine, 1841; Macdonnell, 1858; Wiedersheim, 1887; Stuhlmann, 1889; Parker, 1890-1891; Weltner, 1896). The cocoon is said to be formed by the interaction of the albuminous mucin contained in the secretion of the dermal glands and the constituents of the mud (Walter, 1889). Jardine (1841) states that the lung-fish may live in mud which is exposed and practically dry for 9 months of the year, an estimate which is conservative. Percival ('19) kept 2 fish artificially estivated in dry mud in tin cans for 2 years, and one of these was subsequently put back into mud and induced to estivate a second time.

It is noteworthy that Stuhlmann found *Protopterus* in water ranging as high as 29-37° C. We have kept an estivating fish for 7 days at 40° C., and for a period of 18 days at temperatures above 31.7° C. without injury. These fish are known to estivate in open country, the sun temperature of which may reach 65° C. during the dry season. It seems probable that under these conditions the nest, with its open burrow leading to the surface, may reach temperatures of 37° C. or more for short periods of time, even when 12 to 18 inches underground. It is probable that the mean temperature during the estivating period is 23° C., if not higher. These facts are of interest, since estivation requires that the animal endure starvation and probably complete renal cessation during the hottest part of the year. There is in most parts of Africa where *Protopterus* is found a slight rainfall in every month of the year, and it is probable that even after light rains small quantities of water drain into the burrow, opening as this usually does in exposed horizontal areas, and that this water is available for absorption by the fish.

No excreta are eliminated during estivation. Wiedersheim (1887) states that in a specimen which he dug out of the mud a soft greenish white mass was found outside the cocoon near the opening to the capsule which resembled the excreta of birds and reptiles. Stuhlmann (1889) observed a clear mucilaginous fluid escape from the cloaca of fish estivating in moist ground, but no trace of solid excrements. No other observers describe any evidence of excretion, though one feels sure they would have done so had such evidence been

present. Parker (1890-1891) reports that analyses of the muscles of the estivating fish failed to show any evidence of retention of nitrogenous waste products, but (we call attention to this point particularly) he says the specimens had been active for some weeks, a statement which we interpret to mean that the fish had been returned to water for this time. In which case any re-



FIG. 1. Living African lung-fish, *Protopterus annectens*, brought from Africa in the dry estivating condition. Photograph reproduced by courtesy of the American Museum of Natural History.

tained nitrogenous substance would have been washed out by renewed excretory activity.

That respiration continues during estivation has been shown by Dubois (1892), who has also observed the mechanics of aerial respiration in *P. annectens*. Dubois followed the respiration of the animal while buried in its natural mud nest by connecting the mouth of the burrow with a Marey tambour. He noted that respiration occurred in groups of 2 or more movements separated by long intervals of rest.

The normal aerial respiration, which has been described by Gray (1856) and Dubois (1892), is effected according to the latter as follows:

During inspiration the mouth is opened, the buccal floor is lowered and toward the end of the lowering of the buccal floor, the pharynx and glottis open and air penetrates into the trachea and lungs. Inspiration is effected mechanically by the contraction of 2 dilator muscles of the trachea and especially by

the lowering of the hyoid apparatus at a time when the mouth is wide open. (Dubois speaks of this as "deglutition.") The anatomical structure of the trunk of *Protopterus*, Dubois claims, does not admit the interpretation that inspiration is due to the active dilatation of the walls of the body cavity.

Expiration follows immediately on inspiration and coincides with the beginning of the lowering of the buccal floor. It is produced by the lowering of the hyoidean apparatus and by the contraction of the body walls. It is probable that an active contraction of the pulmonary sac occurs simultaneously with the expulsion of air accumulated during inspiration. In the interval between respirations the animal is in demi-inspiration. The lungs can be filled after the body cavity has been opened but not if one operculum is removed. We have observed that puncture of the lung leads to immediate and repeated swallowing of air, which fact points to the presence of afferent pulmonary nerve fibers. The head will continue to "snap," sometimes for hours, after severance from the trunk; this snapping is apparently a respiratory effort induced by asphyxia.

Macdonnell (1859) suggested that the nostrils (which among the recent fishes lead into the mouth cavity only in the Dipnoi), are used for aerial respiration in the torpid state, rather than the mouth. This is denied by Dubois (1892) as regards normal respiration in air. We have been unable to determine certainly whether or not the nostrils are used for respiration during estivation.

We were not aware in our first experiences with *Protopterus* that this fish is wholly dependent upon aerial respiration, and our ignorance in this respect accounted for the loss of some badly needed specimens at Kisumu. Having once suspected the fact, we set about its demonstration by confining fresh and healthy specimens below the surface of the water.

The fish used in these experiments were about 4 or 5 inches long. They showed no evidence of the external gills which the larvae possess and there is no reason to believe that the results obtained with them are not applicable to larger individuals. One fish at a time was placed in a wide-mouth glass jar, through the top of which a wire frame covered with cheese-cloth was lowered. Running cold water was introduced into the jar by pushing a rubber tube, fed from a water hydrant, through the cheese cloth and nearly to the bottom, the water escaping over the top of the jar. The arrangement was such as to permit free circulation of the water, but to prevent the fish reaching the surface. A 3 to 4 inch cat-fish was placed in the jar with the lung-fish as a control. Under these conditions, as soon as the lung-fish rises for its first breath of air after confinement and discovers that it cannot reach the surface it becomes restless and increasingly active, nosing around the upper edges of the barrier searching for an avenue of escape. This behavior is in marked contrast to the normally sluggish habits of the animal, which usually sinks to the bottom after breathing and remains motionless until the time when it must swim to the surface for another breath. The lung-fish may rest on the bottom for 10

to 15 minutes, but the intervals between its ascents to the top diminish, and within an hour or so it is fighting with vigor to penetrate the obstruction. Developing asphyxia destroys the sense of balance, and the fish swims continuously upon its side or upside down in aimless arcs. It is noteworthy that during this time the rate of branchial respiration, as determined by counting the movements of the gill covers, shows a very marked increase, from once every 5 minutes, or at the most every minute, to once every 2 seconds or oftener.² A branchial respiratory reflex is apparently still present although branchial respiration *per se* is little used and inadequate to maintain life.

The cat-fish control, in the meantime, shows no respiratory embarrassment, and remains quietly on or near the bottom except when disturbed by its harassed companion.

When released from its subaquatic prison before the later stages of asphyxia develop the fish takes several breaths in rapid succession without leaving the surface. For sometime after it remains near the surface breathing at frequent intervals. The branchial respiration has been observed to fall within 2 minutes from 30 to 5 per minute.

In several experiments of this kind the lung-fish died in 2 to 8 hours. A fatal outcome is probably hastened by the struggles of the fish and the variation of the survival time may be due in part to differences in physical activity.

In sharp contrast to this result is the relative subaquatic efficiency of the larval *Protopterus* in which the external gills are still present. We had the good fortune to secure a number of larvae about 3 cm. long. Judging from Budgett's (1899) figures on *P. annectens* they were between 4 and 6 months old. They had 3 pairs of external gills which were 3 mm. long and which projected backward from beneath the gill covers.

Budgett ('03) reports that the larvae of *P. annectens* do not come to the surface for air.

The larvae of *P. ethiopicus* were definitely observed to gulp air, though at very rare intervals. Most of the time they lay quietly on the bottom of the aquarium, or swam around vigorously without coming to the surface. Sections of these larvae show that the lungs are functional.

When below the surface, movements of the mouth, which are apparently respiratory, occur irregularly at 2 to 20 second intervals, and it seems probable that both the internal and external gills are at this time involved in respiration.

When placed in running water and restrained from reaching the surface, they showed no distress for several hours. In the course of a day, however, they congregated at the top and, like the adult, sooner or later put up a vigorous fight for freedom. Some died within 24 hours, and all within 2 days. Confinement is not of itself injurious to them, for we kept some specimens in a few cc. of water contained in a 2 x 20 cm. test tube for several weeks. The fact that they die when prevented from reaching the surface shows that aerial respiration has become a predominant function even before the external gills

² See footnote 2, pp. 165-166.

have disappeared. Under prolonged subaquatic confinement the same increase in movements of the mouth and gill covers were observed as in the adult, indicating that branchial respiratory reflexes are also active before the external gills have disappeared.

The nest of *P. annectens* has been described by Budgett ('03) and Jackson ('16) as an oval shaped hole, 2 to 3 feet in diameter and 18 inches deep. Its vertical walls are lined with a matted network of fine grass roots. Until the land is completely dessicated the nest is filled with water. Around the top is

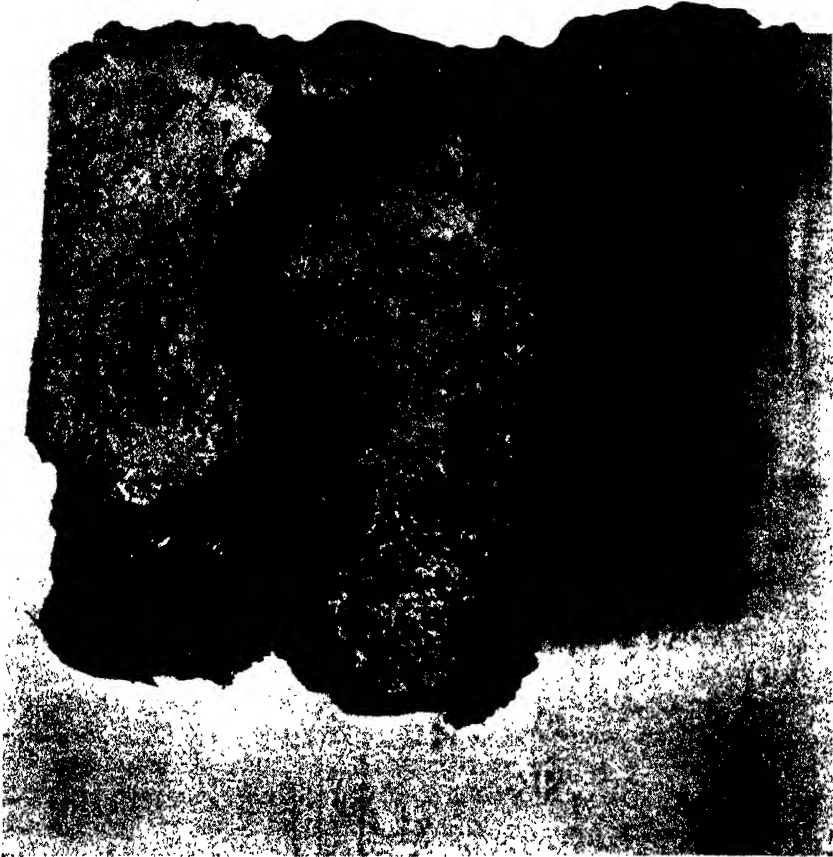


FIG. 2. Estivating African lung-fish curled up in mud removed from glass jar.
Note burrow leading to surface.

a ring of mud, elevated an inch above the water level, and 4 to 5 inches wide, which appears to be deposited by the fish. Presumably the fish, when once stranded by the receding waters, does not leave the nest, for they are not known to travel voluntarily over dry ground (see also Cuninghame, '13). Such information as we have on *P. athiopicus* indicates that the nest is chosen

in the marshes, in 2 to 3 feet of water. Whether or not the fish remain in the nest by preference, so to speak, and deliberately undertake estivation when the waters recede, or whether they are accidentally trapped there, is not known. There is nothing to indicate a general exodus from the permanent bodies of water, in which they may be found the year around, into the marshlands with the advent of the dry season. From such information as is available we are led to the belief that their terrestrial imprisonment is more or less accidental.

In one important respect *P. æthiopicus* appears to differ from *P. annectens*. All the specimens of the latter which have been taken to Europe have possessed external gills incompletely absorbed. Parker's fish ranged up to 80 cm. in length, and out of 100 specimens there were none in which the external gills were not present (see also Ayres, 1885, and Bridge, '22). We have never observed external gills in *P. æthiopicus* in about 150 specimens ranging from 10 cm. up, though they were present in larvae which were about 3 cm. long. It would appear, therefore, that the gills are absorbed much earlier and much more uniformly in *P. æthiopicus* than in *P. annectens*.

The estivating habits of *Lepidosiren*, which have been described by Kerr (1897, 1898), appear to resemble very closely those of *Protopterus*.

Neoceratodus, on the other hand, is not known to undertake estivation or terrestrial life in any form and, in fact, cannot live long out of water (Semon, 1893; Dean, '06, '12a, Spencer, '27; Whitley, '27, '29; Longman, '28). This fish nevertheless makes extensive use of aerial respiration. An aquarium specimen observed by Dean breathed at the surface every 30 to 40 minutes during the day and every 14 minutes at night. Spencer (1892) has suggested that aerial respiration is of greatest value to *Neoceratodus* during the flood season, when the water is riled with sand.

Neoceratodus is considered to be the most primitive, phyletically, of the Dipnoi, but its life habits indicate that it is reverting to a purely aquatic existence, in contrast to *Protopterus* and *Lepidosiren* in which aerial respiration is a persistent, if not an increasingly, dominant mode. In this connection it is significant that the branchial apparatus of *Neoceratodus* approaches in the extent of development that of the teleosts (Gunther, 1871) while in *Protopterus* (Parker, 1892) and *Lepidosiren* (Hyrtl, 1845) the gills are greatly reduced. These facts conform with what is known about the predominance of aerial respiration in the last 2 forms.

In planning our work on these fish we anticipated being able to get them in the estivating as well as in the free-swimming state. Consequently we took with us such chemicals and apparatus as would be required to make analyses of the blood and tissues for nitrogenous and inorganic constituents. Through the courtesy of the local Government officials in Kisumu, a bungalow close to the shore of the Lake was placed at our disposal, and in this a field laboratory was set up.

Unfortunately, we were not able to obtain estivating fish. This was due

partly to an unusually prolonged rainy season, and partly to the fact that the waters of the Lake were at an unusually high level. The mean level of Lake Victoria undergoes, in addition to its yearly cycle, an approximately decennial cycle (Brooks, '25), due to variations in waterfall. The swamp lands around the Lake shore and in the Karno plains East of the Kavirondo Gulf were inundated, as were (by report) all other regions of the Lake shore. There remained a few but very remote arid regions in which estivating *Protopterus* might have been found, but in view of the difficulty of moving the laboratory equipment and the uncertainty of the outcome, it was decided to concentrate on the free-swimming fish at Kisumu and to collect a number of living specimens for transportation to New York where they could be examined more leisurely.

The possibility of transporting these fish alive to New York had been tentatively considered in our earlier plans. But in such instances as were recorded of the transportation of lung-fish from the West Coast to England the fish were collected in the estivating state, dug out with the mud surrounding the cocoon and shipped in this weighty and cumbersome fashion. We were gratified to learn that active lung-fish would live for some time in confinement, in either water or mud. Dr. V. G. L. van Someren of Nairobi, who possesses a wide and authoritative knowledge of the natural history of Kenya and Uganda, informed us that he had induced the lung-fish to estivate by putting them in tin cans filled with semi-liquid mud, and allowing the latter to dry out. Several fish treated in this manner were found alive by him 18 months after burial (see also Percival, '19).

Difficulties were encountered at first in collecting the fish alive. Specimens ranging from 14 to 30 inches are caught by the native fisherman, who use a 5-inch mesh net. As we subsequently learned, *Protopterus* may be asphyxiated in a few hours when kept submerged, and death is no doubt hastened by the struggles of the fish. For this reason few of the fish caught in nets reach the boats alive. When they do come in alive it is the native practice to kill them at once by a blow on the head. *Protopterus* can inflict a serious wound with its sharp teeth and powerful jaws, and the fish when piled indiscriminately with the nets in the bottom of the boat constitute a hazard to bare feet. However, such live fish as we could obtain from this source did not survive more than a few hours, probably because of their weakened condition.

We found that the most satisfactory method of obtaining large fish was by trapping them in the swamps in which they build their nest. Among the Kavirondo natives a few men earn a livelihood by Kamongo hunting. They find the nests among the tall rushes, and, with a good knowledge of the fish's habits, come at the proper hour and tide (a diurnal wind blows a tide of a foot or more into the Kavirondo Gulf) and spear them. These hunters were induced to take the fish for us uninjured by driving them into ambush. Many of these in the early stages of collection did not reach the laboratory alive. They had to be transported several miles and the only available vessels for

carrying them were the earthen-ware pots universally used as household utensils by the natives. The larger of these when filled with water seemed quite adequate for a 2-foot *Protopterus*, but the majority of the fish brought to us in this way failed to survive the journey. In the light of our experiments on respiration this failure was attributed to the fact that the fish were unable to lift their heads out of the water to breathe, and consequently they drowned. This collecting hazard was remedied by having the fish brought to the laboratory in gunny-sacks carried casually over the shoulder, under which conditions they could breathe without difficulty and hence they reached the laboratory in good condition.

Smaller specimens, *i.e.*, under 12 inches, are not caught by the nets, through the meshes of which they can pass without difficulty, and they are rarely seen in the swamps. A source of supply, however, was established in what was virtually our front yard.

A westerly wind blows for the greater part of the day from Lake Victoria

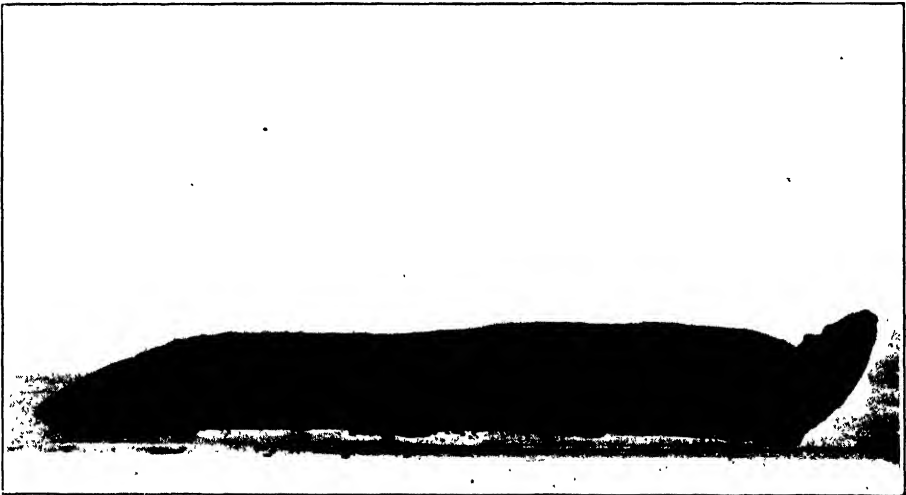


FIG. 3. African lung-fish, *Protopterus annectens*, freshly emerged from estivation. Photograph reproduced by courtesy of the American Museum of Natural History.

into the Kavirondo Gulf. This carries before it floating islands of papyrus which have become detached from swamps near the mouth of the gulf. Many of these islands blow against the shore of the Harbor at Kisumu, impeding navigation and creating a health hazard in mosquito grounds. The Government is consequently constrained to maintain cutters at work removing them almost continuously. The stalks above the water are first cut off and dragged ashore, leaving a mass of roots which will support the weight of several men. The roots are divided into blocks with knives or saws and these blocks are roped and pulled ashore where they are burned. When the roots are pulled apart large numbers of small *Protopterus* (3 to 14 inches), cat-fish

and other inhabitants of the Lake are found entangled in them. The small lung-fish apparently seek the papyrus roots for safety, possibly from their cannibalistic parents.

Papyrus-cutting was going on along the shore immediately in front of the laboratory and through the cooperation of the Superintendent of the Kisumu Prison the lung-fish were gathered up and delivered to us every afternoon.

These small fish were saved from the first in anticipation of bringing them back with us. Except for a few which were put immediately into mud, they were kept in a few inches of water, which was changed every few days. The only information available bearing on the possibilities of transportation was that the fish would live in dried mud, at least if undisturbed. Since the return journey to the East Coast and to New York involved many bumps, it appeared advisable to keep the mud well moistened throughout the greater part of the journey. From our observations in Kisumu it was decided to bring a number in water, in addition to those in mud. As it turned out both methods were satisfactory, though the latter was decidedly more convenient and economical.

We started for New York with 32 one-gallon motor-oil cans of mud, on which a small amount of water was standing; and 8 5-gallon petrol cans with about 6 inches of water. Two to 3 fish were placed in each of the cans of mud, and about 10 small fish, or fewer larger fish, in each of the cans of water. We had, all together, about 150 fish when we left Kisumu.

In loading them in the baggage car for Nairobi, some of the crates were unwittingly piled in the line of draft from the ventilators. Unusually cold weather was encountered the first night as the train passed over Mau Summit (8,500 ft.), and about 40 of the fish which were in water were killed by undercooling. This unfortunate start spoiled an otherwise perfect record; for with the exception of one fish found dead in mud a few days out of Mombasa, and which from the extent of decomposition had probably been dead a long time, no other losses were suffered until after the fish were housed in New York City. The period of transport was about 6 weeks.

This fact alone certifies the remarkable hardihood of these fish. They suffered repeated splashing and jarring; they endured many changes of water including slightly chlorinated water at Nairobi, ship's distilled water at sea and miscellaneous waters taken at various ports; they endured prolonged high temperatures in the tropics, and one box of fish in mud fell 4 feet and was turned upside down in a transcontinental baggage car. They remained for 6 to 8 weeks in tin cans which rusted extensively in spite of a coating of paraffin and which showed in many instances traces of floating oil. During this time they were unfed, since we were convinced they would travel better if the contamination of the water were reduced to a minimum. In short, they survived an ordeal which few other animals, and certainly few other fishes, could have endured without a single casualty attributable to hardship.

Part of the fish were placed in the New York Aquarium, a few being kept in balanced aquaria and the rest in running fresh water at 73° F. (The mean

temperature of Lake Victoria is 73.4° F.) Those placed in balanced aquaria died within several weeks, presumably from infection. Those kept in running water gradually began to eat the beef-heart offered them, abandoned their carnivorous attacks on their comrades and grew for 3 months with surprising rapidity. A broken aquarium window required their temporary removal to another tank containing a single specimen of *Lepidosiren*, also in warm running water, and within a few days the *Lepidosiren* and all the lung-fish died from an infection which ran an unusually rapid course. For practical reasons it was impossible to distribute the lung-fish in a larger number of tanks and thus to circumvent this obvious danger.

We were particularly anxious to study the fish during estivation. Consequently we placed a number of our fish in soft mud contained in glass jars and allowed the mud to dry out. The superficial mud was dry and all free water had disappeared at the end of a month's time. Since all excretion must be completely arrested at about the time the supernatant water disappears, we have arbitrarily dated the beginning of estivation at this date (November 1, 1928). It should be noted that these fish had been starved from about July 15, 1928, or three and a half months prior to the beginning of estivation.

The estivating fish were kept in a cabinet arranged with an automatic heater to keep the temperature from falling below 20° C. No attempt was made to control the humidity of the cabinet nor to keep the temperature at 20° C. when the room temperature was higher.

In the course of time as the mud became increasingly dry it drew away from the sides of the jars and developed large cracks. This contraction was less serious in those jars in which the mud was relatively thick, and our error in obtaining perfect preservation lay in using too thin, rather than too thick, a mixture. As the mud dried the "blow-hole" closed over to an outlet no larger than 1 to 2 mm. in diameter, and in some instances the original blow hole was not visible at all.

A number of fish were removed from mud after 6 to 15 months of estivation, and some of these have been kept in the estivating condition in metabolism chambers for several weeks. Others have been returned to water and subjected to various experimental procedures. Since our chemical and metabolic observations have been published in detail elsewhere (Smith, '30) the present discussion will be limited to a brief summary of the most interesting features.

It appears that during starvation, whether estivating or active, *Protopterus* furnishes about 50 per cent of its metabolic energy by the combustion of fat stored in the body. The remaining energy is furnished by the combustion of the protein of the tissues, probably largely of the skeletal muscles.

Under natural conditions it seems probable that some water becomes available to the estivating fish from occasional rains or moist substrata of earth, but in our experiments the fish have been kept under controlled conditions and have had absolutely no exogenous water for over a year. From this fact, and

from the appearance of the cocoon it is certain that urinary and branchial excretion of non-volatile metabolites is completely suspended during estivation.

The nitrogen of the protein, which supplies in these animals about half the metabolic energy, is of course degraded as the protein is burned; this accumulates in the blood and tissues almost entirely as urea (94 per cent or better). Within a year the concentration of urea in the body (1 to 2 per cent of the body-weight) rises far above that known to occur in any other animal in health or disease, with the exception of the elasmobranch fishes which normally contain large amounts of this substance. Uric acid is apparently decomposed, for only insignificant traces of it can be detected in estivating fish.

When returned to water the fish is apparently awakened by asphyxia, due to its inability to breathe beneath water. Within a few hours it becomes active, breaks out of the cocoon and resumes its normal mode of respiration by rising to the surface for air. For a period of days or weeks the swimming movements of the animal appear to be erratic and incoordinated, as though it had forgotten some of the simple motor acts during its long sleep.

The accumulated urea and other metabolites are excreted rapidly, about 10 days being required to clear the fish of these substances. Because of the tremendous accumulation of urea its excretion during the first few days after the end of estivation may exceed, in proportion to body-weight, that effected by any other known animal.

The fact that *Protopterus* naturally estivates at normal or increased temperatures in contrast to hibernating animals which pass into the quiescent state at reduced temperatures attaches considerable interest to the metabolic rate in active and estivating fish.

Judging the metabolic rate by the consumption of oxygen, we may set the normal level of a starved but active fish at roundly 20 cc. of oxygen per kilogram of fish per hour at 20° C. Of this 20 cc., only 3 cc. goes to such mechanical processes as muscular movements, skeletal muscle tone, circulation and respiration, and the remaining 17 cc. must be ascribed to non-mechanical metabolism, *i.e.*, to processes of an obscure nature, related in part to maintenance of the integrity of the living cells. During estivation the metabolism decreases, falling as low as 5 cc. per kilogram of fish per hour. Of this decrease, of course nearly 3 cc. is attributable to the cessation of muscular activity, for the fish is rigidly imprisoned in its mud nest; the remainder must be attributed to a decrease in the non-mechanical metabolism. There is no evidence that metabolism is specifically inhibited by any of the accumulated metabolites; it appears rather that the protoplasm lives at a lower and lower rate as the tissues become more and more emaciated. This principle of conservation is well known to apply to mammals, but in these it is not so much in evidence as in the lung-fish, perhaps because of the continued activity and higher body temperature of the former.

When the protein of the tissues is burned, the tissue water (which comprises about 80 per cent of the tissue by weight) is discarded and excreted.

In the estivating lung-fish this water is apparently lost by way of the respiratory tract. Certainly none of it is retained by the animal in spite of the fact that the accumulation of urea, etc., leads to a marked rise in the osmotic pressure of the blood and tissues. There is not, however, any evidence that the fish becomes dehydrated during its prolonged sojourn in the mud. The excretion of water by the lungs appears to keep an even pace with the degradation of the water of the tissues and the formation of water by the combustion of protein and fat.

During estivation the fish is in a state of profound sleep, or inhibition, which is apparently of nervous origin induced by postural fixation in the mud, and not in any way due to the uremic state of the animal. This state of sleep is not disturbed by greatly increasing the metabolic rate, by increased temperature, by thyroxin, or by mild sensory stimulation. It is normally terminated, we believe, by the development of asphyxia when the fish is submerged in water.

An interesting comparison may be made between *Protopterus* and man in their relative abilities to endure starvation. In making this comparison we may suppose that a man and a lung-fish enter simultaneously into a period of fasting. Regardless of the differences in their way of life—whether they spend their available energy supply quickly or slowly, actively or quietly—the essential point is how much energy can they get out of the fuel-stuffs stored in their tissues: how many calories can they get from each gram of body-weight which they lose. In both, the energy is stored in the form of carbohydrates, fats or in the proteins of the tissues. In both, the carbohydrate stores are quickly depleted, and for all except the earlier portion of the fast the energy of life must be furnished by fat or by the tissue protein. If the animal chooses to burn fat, since this substance is stored in practically pure form, each gram of body-weight lost will furnish 9.3 calories. If the animal chooses to burn protein each gram of tissue, which contains only about 20 per cent available protein, can furnish only 0.9 of a calorie. It follows that the storage of energy in the form of fat is about 10 times as economical as in the form of protein.

Even when plenty of fat is available, *Protopterus* obtains nearly 50 per cent of its energy from protein, whereas a fasting man as a rule obtains only 15 per cent of his energy from this substance. Consequently *Protopterus* derives but 1.6 calories, while man derives about 4.0 calories from each gram of body-weight lost. Thus, his higher fat combustion makes man a better prepared candidate for fasting by a ratio of 2.5 to 1. If they both die when they have lost 50 per cent of their respective body-weight, man is good for 2.5 times as many calorie-hours as the lung-fish.

Prolonged starvation is an ordeal to which every animal is at some time or other subjected. It was somewhat of a surprise to us to find that *Protopterus*, which has been systematically practicing this ordeal, so to speak, since the Devonian period should choose to live upon its body tissues in preference to the

more economical medium of fat. There is some evidence that the difference between *Protopterus* and man, as roughly sketched above, distinguishes warm and cold-blooded animals generally. It may be that a greater capacity to store, transport and utilize fat is a concomitant of the evolution of homoiothermy; or it may be that in the obscure chemical metabolism of the lung-fish there is a reason that renders the extensive combustion of protein a necessary or a sound procedure.

In any case, *Protopterus* meets the emergencies of an uncertain life in an admirable way. If we exclude the unavoidable dangers of infection incidental to a strange habitat, it would appear that they can claim a place among the hardiest of animals. They can survive temperatures as high as 40° C.; they can endure without food for long periods of time; they are completely independent of the respirable quality of the water in which they live; they can tolerate the complete cessation of kidney and other excretory function, and, though they cannot live long if completely submerged under water, they can—when invested by the cocoon of estivation—live out of water and without water for a period of months or years.

If we are permitted to view the ancestors of the terrestrial vertebrates as physiologically similar to *Protopterus*, we cannot help feeling that they started out in their new way of life with a magnificently robust inheritance.

SUMMARY

Specimens of *Protopterus aethiopicus* were collected from Lake Victoria and brought to this country alive for physiological and biochemical investigations. A number of these were induced to enter into estivation under controlled conditions in the laboratory.

The external gills atrophy earlier and more completely in *P. aethiopicus* than in *P. annectens*. *P. aethiopicus* is dependent upon aerial respiration, the internal gills being inadequate to maintain life. The lungs become functional and necessary to life before the external gills have disappeared, although branchial reflexes are present and increased branchial activity is evoked by asphyxia in both the larvae and the adult.

Estivating fish are known to survive for 18 months and estimates based upon metabolism data indicate that they may survive much longer periods. During this time they can live entirely without exogenous water and food, although pulmonary respiration continues.

Biochemical observations on estivating and active fish are reported elsewhere, but it may be noted here that estivation is accompanied by a marked reduction in metabolic rate which is apparently related to progressive emaciation, by the complete cessation of excretion of non-volatile metabolites and by the appearance of a state of sleep or nervous inhibition which is possibly induced by postural fixation but which is not related to temperature, metabolic rate, sensory stimulation or the retention of metabolites. When reimmersed in water the estivating fish is apparently awakened by asphyxia.

The literature on the life habits of *Protopterus* is reviewed.

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RELATION OF LATITUDE TO TIME OF BLOOMING OF TIMOTHY¹

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If the time of blooming and maturing of any species of plants were recorded, at a series of stations located over a wide range of latitude, and if all conditions excepting those dependent upon latitude were uniform, in what way would the season of blooming and maturing be found to progress from south to north?

According to Hopkins' Bioclimatic Law, as it was stated in 1918, the time of blooming of any plant should progress from south to north, at stations on the same degree of longitude and at the same altitude, over the entire range of latitude, at the uniform rate of one-fourth of a degree of latitude each day (Hopkins, '18, p. 7).

Two years after this Law was published, Garner and Allard ('20) announced the results of a series of investigations, in which they discovered the phenomenon of plant response to length of day. They found that there is something in the effects of the length of the period of daily illumination, independent of any effect which the length of day may have upon temperature, which has a vital relationship to the life processes of many plants. Some plants, known as "long-day plants," require a relatively long day for the formation of inflorescences and seeds; when the days are short, they make vegetative growth only. Other plants, known as "short-day plants," make a vegetative growth only, while the days are long, and they do not produce flowers and fruit until that season of the year when the days become relatively short and the nights long. Late-flowering cosmos is a typical short-day plant. There is a third class of plants which, at least under certain conditions, seem indifferent in their response to photoperiodic influences, and in which the life processes are completed within a given time, irrespective of the natural changes in length of day and night.

Timothy (*Phleum pratense* L.) is an example of a long-day plant. Growing under natural conditions, stems or shoots which develop from seeds or buds during midsummer produce leaves, but usually no formation of culms through elongation of internodes of the stems, and no development of inflores-

¹ This study was planned at, and the plants were distributed from, the Timothy Breeding Station, North Ridgeville, Ohio, which is conducted cooperatively by the United States Department of Agriculture and the Ohio Agricultural Experiment Station.

Hopkins, A. D. The Bioclimatic Law. U. S. Dept. Agri. Weather Bureau; Monthly Weather Review Supplement No. 9; pp. 1-42; 1918.

cences occurs, either during the remainder of that season or during the first few weeks of spring in the following year. Later in the spring, when the days become longer—about May 1 in the latitude of northern Ohio—vegetative development from the growing points of the more vigorous shoots ceases, and inflorescences form.

If, at the time in the fall when growth in the field is about to cease because of cold weather, timothy plants are transplanted to a greenhouse where conditions for growth are favorable, and where there is no illumination in addition to that received from the sun, the plants will continue their vegetative growth during the winter, producing new leaves at intervals of about 8 or 9 days—but there is no development of inflorescences in the greenhouse until nearly the same time in the spring when these processes occur in the fields in plants which have been practically dormant for weeks or months. However, if a 200-watt electric light, placed about 3 feet above the plants in the greenhouse at any time during the winter, illuminates the plant from dusk to about midnight each day, so that the total daily period of illumination is approximately the same as in the latter part of spring and early summer, the internodes of the culm become elongated and inflorescences form within a comparatively short time (Evans, '27, pp. 45-49).

In the extreme southern part of the United States, growth of timothy plants continues during practically all of the winter months, and, as far as temperature conditions are concerned, the weather is suitable for the development of inflorescences and seeds very early in the spring. In a location as far north as Fairbanks, Alaska, on the other hand, growth does not begin until sometime in the spring. At northern latitudes, within a few weeks after spring growth of timothy has begun, the length of day is considerably greater than it was in very early spring, when the timothy plants in the south were already making a vigorous vegetative growth. With the knowledge that we now have of the susceptibility of timothy to the length of day, in relation to the development of the inflorescence, the question arises as to whether the northward movement of the blooming season of timothy would not be greatly affected by these differences in the lengths of day.

In 1927, timothy plants of two different selections or strains, an early-maturing one and a late one, were sent to stations located along a line which may be roughly described as extending from southeast to northwest; Savannah, Georgia, was the most southern station, and Fairbanks, Alaska, the most northern one from which records were obtained. The plants were propagated vegetatively, by separating clons from the original plant of each selection; plants propagated in this way may be regarded as identical in their genetical composition. In 1928, records were obtained of the dates when the first florets bloomed on each plant of timothy No. 11902² at 6 stations. Similar records were obtained again at each one of these stations in 1929, and also

² F. C. numbers 11902 and 12421 assigned, by the Office of Forage Crops and Diseases of the United States Department of Agriculture, to 2 selections of timothy plants.

from some additional stations to which plants had been sent in 1928. The data from both selections are presented in Table I. The records from the 6 stations where dates when the first florets of timothy No. 11902 bloomed in both seasons are shown in graphical form in figure 1.³

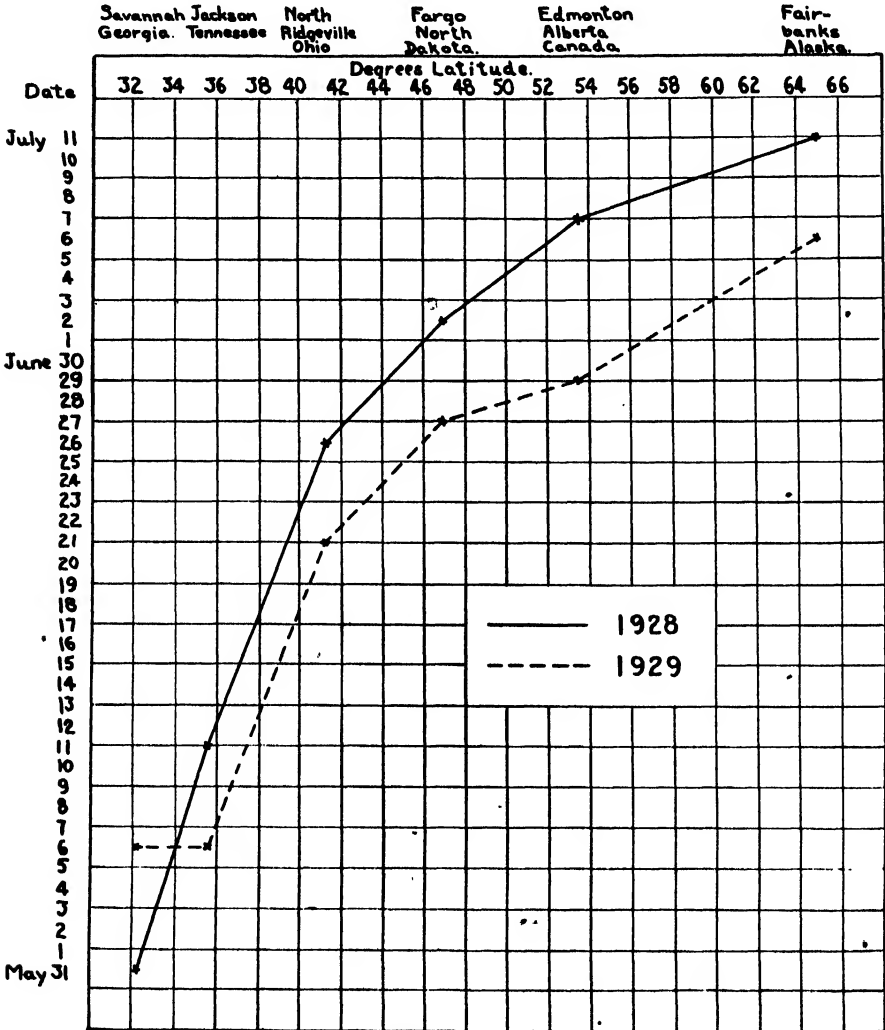


FIG. 1. Dates when the first florets bloomed in 1928 and 1929, on plants of timothy No. 11902, at stations located at different latitudes.

³ This experiment is one of the type which can be conducted only through the co-operation of a considerable number of observers. The writer wishes to acknowledge his indebtedness not only to those observers whose records are presented in this report, but also to others who have grown the plants in localities where, because climatic conditions are not suited to timothy, or where for some accidental cause, no records of blooming have yet been obtained.

TABLE I. *Records of dates when the first florets bloomed on plants propagated vegetatively from the original plants of timothy selections, No. 11902 (early), and No. 12421 (late), at different stations where they were growing in 1928 and 1929*

Station	Latitude		Date first florets bloomed			
	Degrees	Minutes	No. 11902		No. 12421	
			1928	1929	1928	1929
McNeill, Miss	30	40				
Savannah, Ga	32	6	May 31	June 6		July 14
Jackson, Tenn	35	37	June 11	June 6	July 2	July 5
North Ridgeville, Ohio..	41	23	June 26	June 21	July 5	July 6
Ames, Iowa	42	2		June 18		July 1
Redfield, S. D	44	52		June 19		July 6
Fargo, N. D	46	52	July 2	June 27		
Saskatoon, Saskatche- wan, Canada	52	15		July 10		July 15
Edmonton, Alta., Can- ada	53	33	July 7	June 29	July 11	July 8
Beaverlodge, Alta., Can- ada	55	10		July 2		July 10
Sitka, Alaska	57	3		July 27		Aug. 2
Fairbanks, Alaska	64	51	July 11	July 6	July 15	

One of the conclusions stated as part of Hopkins' ('18) Bioclimatic Law is that: "Other conditions being equal, the variation in the time of occurrence of a given periodical event in life activity in temperate North America is at the general average rate of 4 days to each one degree of latitude, 5 degrees of longitude and 400 feet of altitude, later northward, eastward and upward in the spring and early summer, and the reverse in late summer and autumn." If the dates at which timothy plants began to bloom at North Ridgeville, Ohio, are used as a base, it will be found that, according to the preceding statement, the actual time of blooming at the southern stations was later, and at the northern stations earlier than it should have been. According to the United States Geological Survey, Fairbanks, Alaska, is $32^{\circ} 46''$ of latitude north of, $66^{\circ} 39''$ of longitude west of, and at an elevation of 471 feet higher than Savannah, Georgia. Using these figures, one may calculate that timothy plants should bloom 82 days later at Fairbanks than at Savannah; actually, there was a difference of only 41 days in 1928, and of only 30 days in 1929.

If the time of blooming progressed from south to north at a uniform rate, the dates would be recorded on the graph in fig. 1 as a straight line. The actual records for 1928 are represented by a curve which shows that the blooming season passed from south to north at a constantly accelerated rate. The corresponding records from the same stations in 1929 do not make quite such a well-formed curve, yet it resembles the 1928 curve much more than it does a straight line.

There are a number of exceptions shown in Table I to the general tendency indicated by the 1928 curve in the graph. For instance, in 1929, the plant No.

11902 bloomed 2 days earlier at Redfield, South Dakota, than at North Ridgeville, Ohio, although Redfield is $3^{\circ} 29''$ north of North Ridgeville. The 1929 records show that at McNeill, Mississippi, the plant No. 12421 did not bloom until July 14—only one day earlier than the plant of this number bloomed at Saskatoon, Canada. The observer at McNeill reported that the plant did not appear to be making a normal growth, and it is probable that the apparently delayed date of blooming may be attributed to some unfavorable condition of soil or climate. Two timothy plants, propagated vegetatively from the same original plant, and grown in the same location, but under different cultural conditions, may bloom at different dates. At Savannah, Georgia, the plant of 11902 bloomed 6 days later in 1929 than in 1928, though at all other stations from which records were obtained in both seasons the plants of this number bloomed several days earlier in 1929 than in 1928. These seasonal differences in time of blooming are probably correlated, to some extent at least, with variations in weather conditions.

Of course, Hopkins' Bioclimatic Law is far more complex than the preceding discussion might seem to indicate. Other varying factors in addition to those of latitude, longitude, and altitude, must be considered. Hopkins ('18) states: "The variations in the climate and consequent variations in the geographical distribution and periodical activities of the plants and animals of a continent are controlled by the modifying influences of topography, oceans, lakes, large rivers, and of other regional and local conditions, and the amount and character of daylight, sunshine, rain, snow, humidity and other elements and factors of a general and local nature." Although he refers to "the amount and character of daylight" as one of a large number of controlling factors, he does not give it the relatively important position which it seems to possess.

This paper should by no means be regarded as an unfavorable criticism of Hopkins' Bioclimatic Law. The conclusions which this law represents are based on a vast number of authenticated facts; and it probably correctly describes many phases of life activity in their relations to latitude, longitude, and altitude. However, the evidence which has been presented here seems to indicate that, as it is stated, the important effects of the factor of photoperiodism are not recognized. Consequently, some phases of the life history of some plants, as they are affected by seasonal changes, apparently are not adequately described by the Bioclimatic Law.

The results of this experiment should be regarded as suggestive, rather than conclusive. A few records are difficult to understand, even if allowances are made for the unequal conditions at the stations where they were obtained. However, the value of the experiment depends not on the exceptional records, but upon the general trend of the records from all of the stations.

The experiment which has been described suggests the following hypothesis: *The season of blooming of timothy, in the northern hemisphere, progresses*

from south to north at a constantly accelerated rate, due to the gradually increasing length of day, from southern to northern latitudes, at the time when the inflorescences develop. Whether this hypothesis may become an accepted theory will depend upon the results of more extensive field experiments, and of study, under controlled conditions, of the effects of variations in length of day, temperature, and of other factors, upon the growth of timothy.

SUMMARY

This paper describes an experiment in which the time of blooming of timothy was recorded at stations at different latitudes. Plants were grown at a series of stations extending from Savannah, Georgia, to Fairbanks, Alaska.

The plants growing at the southern stations bloomed later, and those at the northern stations bloomed earlier than would be expected from Hopkins' Bioclimatic Law. At the southern stations, although temperature and soil conditions permitted growth very early in the spring or even to some extent during the winter, inflorescences did not form and florets did not bloom until the season when length of day was approaching the maximum. At the most northerly stations, where the plants were dormant during the winter and early spring, inflorescences formed and florets bloomed after a much shorter period of spring growth than in the case of the plants at the southern stations.

The following hypothesis, based on the results of this experiment, is offered: *The season of blooming of timothy, in the northern hemisphere, progresses from south to north at a constantly accelerated rate, due to the gradually increasing length of day, from southern to northern latitudes, at the time when the inflorescences develop.*

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STUDIES IN THE ECOLOGY OF FOREST COLEOPTERA—II

THE RELATION OF CERTAIN COLEOPTERA TO PLANTS FOR FOOD AND SHELTER, ESPECIALLY THOSE SPECIES ASSOCIATED WITH FUNGI IN THE CHICAGO AREA

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Introduction

Evidence has been presented elsewhere (Park, '30) indicating that the forest Coleoptera inhabiting the Chicago area form both seasonal and seral succession communities, and further that these communities correspond in general to the plant associates of the plant forest sere of the same region.

Illumination data gathered over 3 consecutive years in the unshaded areas, and in the pioneer cottonwood, pioneer conifer, black oak and climax maple communities of the upland forest sere of the Chicago area (Park, '28) show a close correlation between (1) the intensity of daylight penetrating to the forest floor, (2) the amount of floor shaded, and (3) the ecological or seral succession of these communities of plants. This work will be published in detail later (Park, '31).

These illumination data make it advisable to reexamine the relationship between the plant communities of this area and some faunal unit in an attempt to see whether or not animal communities, as represented by some distinct element thereof, are related in their distribution primarily to the plant constituents or to the physical factors associated with intensity of illumination.

Any one of a number of faunal groups might have been taken as the basis of this study so far as general relationships are concerned. Since best results could be obtained by selecting a group with which the investigator is taxonomically familiar and which is well represented in the literature, it has seemed desirable to use again the Coleoptera in testing out the relationships suggested above.

Using the beetles then, as a test group, their distribution in this area will be considered in the light of their relationship to their food plants in general and to a specific set of food plants, the fungi, in particular.

The Indirect Rôle of Daylight in the Ecology of Forest Beetles

Data are available from a study of food plants, and from shelter studies, to show that light acts indirectly, through plant life, in affecting the distribution of beetles.

The evidence shows that possibly seasonal and seral succession of beetles

may be directly correlated with food, and only secondarily with such physical factors as light. For this survey of the problem the herbivores offer many advantages. The species associated with carrion and with dung are obviously not relevant to this discussion. The carnivores have also been omitted since they have a wider range as a rule (save where special food habits may limit their activity, as in the cychroid carabids with snail-eating proclivities). Many of these flesh-eaters depend directly upon the herbivores for food, and their distribution may be either closely or loosely related to that of their food species.

Only a few herbivores have been chosen from a great many. The data following have been drawn from notes on important species whose feeding behavior or food has been observed by the writer, and with few exceptions the habitat and community relations of the several food plants have been substantiated by Fuller ('25). It is unfortunate that no general phenological data exists for the plants of the Chicago area;¹ consequently the leafing out, flowering period, fruit and seed periods, et cetera, have of necessity been drawn from my own field observations where possible.

In the following section, the upland forest sere of the Chicago area is arranged with respect to the advancing mesophytism of the index species of plants, and such natural grouping has been found to be closely correlated with the amount of daylight penetrating to the forest floor, as mentioned previously (Park, '28).

I. PIONEER COTTONWOOD ASSOCIES (FULLER, 1925: I, —3)

Populus deltoides Marsh.

Plectrodera scalator (Fab.), beaten from foliage of saplings on July 19 and 20, and August 20. Blatchley ('10, p. 1068) finds it from "August 6–September 19. Occurs in the sand dune region, where it probably breeds in the quaking aspen and cottonwood, both of which are fairly common in that area." Felt ('06, II, p. 746) gives the species as breeding in poplar and willow, and Beutenmuller (1896, p. 78) says of this species that it "bores in the roots of cottonwood and willow."

Oberea schaumii Lec., beaten from foliage between June 24 and July 8. Blatchley ('10) and Felt ('06) find the larvae in the twigs and branches of poplar, the adults appearing from May 24 to June 23.

Metachroma interruptum (Say), *M. angustulum* Cr., and *M. parallelum* Horn, were taken in numbers from cottonwood foliage from June 24 to July 10.

Lina lapponica (Linn.) and *L. scripta* (Fab.) were taken from cottonwood foliage from the end of April to July 26. These 2 chrysomelids are discussed by Blatchley ('10) and Felt ('06) at some length.

Disonycha quinquevittata (Say), taken from April 26 to September 30; Blatchley ('10) finds it from May 6 to September 7 in numbers in the Indiana dune region on the foliage of certain willows and cottonwoods.

Salix.²

Disonycha quinquevittata and the 2 species of *Lina*, noted above, have been men-

¹ Personal communication from Dr. George D. Fuller, The University of Chicago.

² A number of species of willows, especially *S. longifolia* Muhl., *S. syrticola* Fern., *S. glaucophylla* Bebb, and *S. humilis* Marsh.

tioned for the cottonwoods, and the records apply for the willows of this associes as well. *Lina lapponica*, however, is a typical leaf-feeder on the willows, and deserves special mention. Adults have been observed hibernating beneath mesophytic floors of the climax forests in April and early May, and are usually active upon willow foliage of the pioneer cottonwood associes from April 12 to August 15. Its maximum abundance comes in late July usually, when adults are not only actively feeding and copulating, but are being constantly joined by freshly pupated, pale individuals from the pupae cases attached to the leaves of the food-plant. *Lapponica* is further treated by Felt ('06), II, pp. 564-565).

Calligrapha bigsbyana (Kirby) has been taken on willow foliage from August 20 to 25 which is well within the range assigned to it by Blatchley ('10), and Hegner ('08, '10) has found it feeding on *S. longifolia* in nature, and upon both *S. longifolia* and *S. amygdaloides* in the laboratory.

These are but a few of the many species of leaf-feeding beetles which could be cited as having their food within the pioneer cottonwood associes through a definite seasonal range corresponding with the seasonal duration of food-plant foliage.

II. PIONEER BLACK OAK ASSOCIES (FULLER, 1925: I, —5)

Quercus velutina Lam.

Serica sericea (Ill.) occurs throughout Indiana, according to Blatchley ('10, p. 958), under various kinds of shelter, and hibernates beneath partly buried logs in the pupal condition. Data accumulated on this species for 5 years give its range in the Chicago area as from April 25 to July 23, or from the time when the black oaks are beginning to leaf out until the height of foliation. The adults feed on the leaf epidermis of the black oak. In April they have emerged and are ending the winter in a state of semi-hibernation in the leaf mould of mesophytic forest floors, together with many other species having a similar rhythm.

Pandeleteius hiliaris (Hbst.) has been taken hibernating beneath logs on the forest floor, and is beaten in numbers from the foliage of black oak from May 23 to July 23. Its occurrence on the related scarlet oak, as well as black oak, is mentioned by Blatchley and Leng ('16, p. 120).

Ceanothus americanus Linn.

A number of species have been observed on New Jersey tea in the dune region of Indiana and Illinois, the shrub being very common in the black oak associes. Among these may be mentioned the mordellids, *Mordella melaena* Germ. (July 10-16), *M. atrata* Melsh. (July 8-23), *M. a. lecontei* Csi. (July 16-23), *M. octopunctata* Fab. (July 10-16), *M. marginata* Melsh. (July 8-23); the clerids, represented by *Trichodes nutalli* Kby., are also abundant on the flowers from July 12-23; the alleculid, *Isomira sericea* (Say) (July 8-31); the buprestid, *Acmaeodera pulchella* (Herb.) (July 12-23); the cerambycids, *Batyleoma suturale* (Say), *Typocerus velutina* (Oliv.) from July 8 to 23, and many other species of Coleoptera.

It will be seen that these 12 species visited flower clusters of *Ceanothus* between July 8 and 31, the approximate period of flowering for this plant in the Chicago area, although the actual range probably extends a few days on each side of these dates. That *Ceanothus* attracts a number of anthophilous Coleoptera is well known (Robertson, 1889; Morris, '09; Blatchley, '10; Banks, '12). The seasonal range of the above species of beetles, as given by Blatchley, generally coincides with the seasonal range as determined by the writer in the Chicago area, usually including enough margin on either side of the flowering range to coincide with the general period of the year in which a number of associated plants are blooming in succession in the black oak associes.

Tradescantia virginiana Linn.

Lema collaris Say has been observed on the flowers of the Spiderwort from June 15

to 23. This species was taken copulating, on its food plant, on June 15 and 25. The adults emerge near the last of July, at least in one series of observations, so that 2 broods may be the rule. They emerge from white, elongate-oval cases attached to the leaves and stalks of the plant, and apparently attack the flowers, especially the unopened buds, by making a small, rounded hole through the soft petals. This species has been observed alive in the lower beach drift of Lake Michigan as early as May 19, probably early ex-hibernants, and the first brood may occur early in the summer. Blatchley finds *collaris* from May 11 to July 1 on spiderwort and other herbs in moist, sandy areas, and I have taken it from the butterfly-weed (*Asclepias tuberosa* Linn.) in the same associates from July 8 to 12 in the orange flowers. Robertson (1892) found the spiderwort blooming from May 22 to July 30, and visited by insects on June 4, 5, and 12.

Helianthus species.

A number of beetles occur regularly on the flowers of this common composite, of which may be mentioned *Mordella melaena* Germ. (July 29), *M. atrata* Melsh. (August 10), *Acmaeodera pulchella* (Herbst.) (July 29), *Batyloema suturale* (Say) (July 29-August 8), *Diabrotica duodecimpunctata* (Fab.) (September 11), *D. longicornis* (Say) (September 14) and *D. vittata* (Fab.) on September 11.

It is interesting to note how an herb with a long flowering range, as the daisy, serves to bridge over the gaps in the flowering season of other plants which bloom for only a limited period and consequently affect the distribution of flower-visiting beetles. Robertson (1898) found *Helianthus divaricatus* Linn. to be visited by anthocoles at Carlinville, Illinois, on August 8, 14, 17, 21, 24, 27, 28, 29, 31 and on September 2, 4, 7, and 10. During this period other herbs in the Chicago area began and ended their blooming period on the floor of the black oak associates.

Spiraea latifolia Boekh.

The meadowsweet is another attractive flowering herb as far as the Chicago area Coleoptera are concerned, and the more common species may be cited as occurring on the fragrant blossoms: *Mordella octopunctata* Fab. (August 8-10), *Typocerus velutina* (Oliv.), *Ophistomis luteicornis* (Fab.) and *Cryptoccephalus mutabilis* Melsh.

Euphorbia corollata Linn.

Mordella atrata lecontei Csi. occurs on the blooms of the flowering spurge between July 16 and 23. Robertson (1896) found this herb to bloom from May 24 to September 27 and to be visited by Diptera, and a few Hymenoptera and Hemiptera during this period.

Rudbeckia hirta Linn.

Mordella marginata Melsh., *Trichodes nutalli* Kby., *Batyloema suturale* (Say) occur on the flowers of this composite from July 8 to July 23, the clerid being more common here towards the end of the range, and the mordellid and cerambycid toward the beginning of the range as given here.

Solidago hispida Muhl.

Occurring on the flowers of the rough goldenrod may be mentioned *Diabrotica duodecimpunctata* (Fab.) and *D. vittata* (Fab.) from September 11 to 30, *Epicauta pennsylvanica* (DeG.) both on the flowers and stems from August 15 to September 14, and copulating frequently over this range which serves to overlap the range of the ubiquitous chrysomelids. *Euphorbia sepulchralis* (Fab.) occurs later on the goldenrod flowers, from September 20 to 24 according to the data collected. This species of herb, like so many others which might be mentioned here, occurs both in the black oak associates and along its tension lines, as well as in secondary communities such as borders of fields and roads, so that it tends to have a varied and fluctuating population.

Rosa humilis Marsh.

Visitors of the wild rose have not been observed as closely as desired, but we may cite the cerambycids, *Ophistomis luteicornis* (Fab.) and *Typocerus velutina* (Oliv.), as both feeding and copulating here on July, 12 in numbers.

It will be seen that some anthocoles are more narrowly restricted to food-plants than others in certain associates, and some species occur on a great variety of flowers over a long flowering range. Thus the common *Typocerus velutina* (Oliv.) apparently has catholic feeding habits being found on many plants not listed here, e.g., *Cirsium arvense*.

It is the belief of the writer that we would be in a much more intelligent position concerning the fundamental nature of communities if the feeding range and behavior of the inhabitants were even partially understood, since we contend that under natural conditions many species are limited only indirectly by the important physical factors and more directly by such agencies as food and shelter.

With reference to what has been said, it is interesting to examine a few species of anthocolous Coleoptera with respect to their food habits. In Table I the 5 most common species of *Mordella* in the Chicago area are given with their observed average distribution on the flowers of 5 common herbs which are found throughout the pioneer black oak associates of this area, especially in the small, sunny clearings.

TABLE I. *Mordella* and associated food-plants

<i>Mordella</i>	<i>Ceanothus</i>	<i>Helianthus</i>	<i>Spiraea</i>	<i>Euphorbia</i>	<i>Rudbeckia</i>
<i>melaena</i> Germ.	July 10-16	July 29			
<i>atrata</i> Melsh.	July 8-23	Aug. 10			
<i>atrata lecontei</i> Csi. . . .	July 16-23			July 16-23	
<i>octopunctata</i> Fab.	July 10-16		Aug. 8		
<i>marginata</i> Melsh.	July 8-23				July 8

From the records in Table I, even in their limited extent, it will be seen that all 5 of the mordellids are commonly taken on *Ceanothus* in its flowering range. In 3 of the 5 species of beetles, their presence in the black oak associates is further prolonged from 1 to 2 weeks due to the flowering of other herbs in succession after *Ceanothus* has passed its maximum period of attraction. After August 8 no other herb apparently attracts these species with its flowers, and by this time the individuals have either died or joined others of their species in neighboring meadows and secondary associates where other herbs may still be in flower. Although variations in this routine are obvious, and the data could be extended indefinitely by further observation, the material would seem to indicate the important rôle of food-plants in determining the distribution of certain herbivora in the upland forest sere during the growing season. Without repetition of detail, the same may be said of many other herbivorous Coleoptera, e.g., the anthocolous cerambycid, *Typocerus velutina* (Oliv.), et cetera.

III. MESOPHYTIC OAK-ELM-HICKORY SUB-CLIMAX (FULLER, 1925: I, —6, VII)

Carya cordiformis Koch.

Saperda tridentata Oliv. has been beaten from the foliage of the bitter-nut hickory in numbers on July 17, and this is in the seasonal range for the species as given by Blatchley ('10, p. 1087). It has been repeatedly beaten from elm foliage. The larvae bore into this tree (Felt, '06, I, pp. 67-71).

Carpinus caroliniana Walt.

Astylopsis macula (Say) has been beaten from the foliage of blue beech, and taken beneath its bark on July 17. Blatchley ('10, p. 1072) gives the range of this species as from May 27 to June 24. He has taken it from the bark of walnut, from the foliage of oak, and finds it breeding in beech, hickory, black walnut and butternut, so that *macula* would seem to have a variety of food and breeding habits, yet the trees frequented are found regularly within the leafing period of the sub-climax communities of the upland forest sere.

Aegomorphus decipiens Hald. has also been taken from the bark and foliage of the

blue beech on July 17, and this niche is confirmed by Champlain, Kirk and Knull ('25) who note that adults could be reared from linden, tulip, black ash, sweet cherry, and blue beech.

On the same date, the weevil, *Acoptus suturalis* Lec., was taken from the foliage of blue beech in numbers, and this habitat niche is confirmed by Blatchley and Leng ('16, p. 424).

Vitis vulpina L.

Although this climber thrives in the more pioneer communities of the upland forest sere as well as in the sub-climax forests and secondary communities, certain species of Coleoptera may be mentioned here. Among these may be noted *Pelidnota punctata* (Linn.), the grape scarab, as having been taken from the foliage as late as August 11, even copulating at this time, and Blatchley ('10, p. 986) finds the species throughout Indiana on both wild and cultivated grape.

The grape cerambycid, *Phymatodes amoenus* (Say), has been beaten from the foliage and stems of wild grape on June 25. Blatchley ('10, p. 1018) found it from May 11 to June 5 by beating wild grape, and Beutenmuller (1896) also noted the species boring in the dead wood of the vine.

Viburnum.

A number of species of *Viburnum* occur in the sub-climax associates, the flowers apparently having many coleopterous visitors. Among these may be cited the cerambycids, *Acmaeops nigripennis* (Lec.), *A. n. varians* (Lec.), *Brachyleptura rubrica* (Say), and *Strangalepta lineola* (Say) between June 14 and 25. The flowering range and some of the anthocolous Coleoptera frequenting several species of *Viburnum* at Carlinville, Illinois, are mentioned by Robertson (1898).

Apocynum androsaemifolium Linn.

The chrysomelid, *Chrysochus auratus* (Fab.), is commonly taken from the foliage of the spreading dogbane from July 5 to September 24 in the Chicago area, and frequently in or along the ecotone of the sub-climax communities. Blatchley (*loc. cit.*, p. 1141) finds it throughout Indiana from June 11 to August 10 on this herb. The relation between *Apocynum* and *Chrysochus* is well known, and the life-history of the beetle is intimately bound up with its food-plant, data on which are given by Weiss and West ('21) and E. M. Craighead ('23).

Laportea canadensis Gaud.

The foliage of the wood-nettle is commonly a characteristic of the herbaceous stratum of both climax and sub-climax floors, and frequently supports a number of the chrysomelid, *Anoplitis inaequalis* (Web.). In the Chicago area this chrysomelid has been so taken from June 22 to August 26, copulating throughout this range, and Ouellet ('19) found it under similar conditions on *Solidago latifolia* Linn.

Polygonatum.

The anthocolous cerambycid, *Strangalepta lineola* (Say), was taken from the flowers of Solomon's seal on June 7.

Heracleum lanatum Michx.

A number of Coleoptera visit the cow parsnip in June, and Gray ('08, p. 621) notes this month as being the period of flowering. Among these species may be mentioned *Acmaeops bivittatus* (Say), *A. nigripennis varians* (Lec.), *Strangalepta lineola* (Say), *S. pubera* (Say), *Molorchus bimaculatus* Say, and *Diabrotica vittata* (Fab.) being taken from the flowers in numbers on June 7.

Zizia aurea Koch.

Mordellistena bipustulata Hell., taken on the flowers of the Golden Alexander on June 7.

Many plants occur in the marginal zone of the sub-climax as well as the sub-climax ecotone and the neighboring secondary communities. The distribution of such species is difficult to plot due to this ecological tolerance, and these plants support a large, if fluctu-

ating, fauna of anthocolous Coleoptera. The fleabanes (*Erigeron*), blooming from April to August, belong here apparently, and during this period are visited by many beetles found typically in secondary communities, as well as species more commonly noted in the forest sere, and the ever present ubiquitous species which have a wide range of food plants.

We may mention also in this category the ragweeds (*Ambrosia trifida* L. and *A. artemisiifolia* L.), especially in connection with the carabid genus *Harpalus*. *Harpalus caliginosus* (Fab.), *H. erraticus* Say and *H. pennsylvanicus* DeG. have all been noted eating the blackish ragweed fruit between August 25 and September 19, in the Chicago area, and their feeding habits have been treated generally by Forbes (1883, 1903) and by Webster (1903). This is also the copulation period for *caliginosus*, and *pennsylvanicus* has been taken copulating on September 11.

IV. CLIMAX MAPLE ASSOCIATION (FULLER, 1925: I, —7)

Acer saccharum Marsh.

Attelabus bipustulatus Fab. has been taken from the foliage of the sugar maple on May 7, and Blatchley and Leng ('16, p. 63) give the range of this weevil as May 6 to July 25, finding it on the foliage of a number of climax and sub-climax trees.

The maple borer, *Plagionotus speciosus* (Say), although characteristic of the climax maple, has not been taken by me in the Chicago area, though it doubtless occurs and has been discussed by Blatchley ('10, pp. 1034-1035), Felt ('06, I, pp. 51-56), Packard (1890, pp. 374-379) and by Beutenmuller (1896, p. 77).

The herbaceous stratum of the climax forest supports many beetles, and the records could be extended without bringing any essentially new points of view to what has been said. The rich fungoid flora, and the associated Coleoptera, so typical of the dark, moist climax floor will be discussed later.

In the preceding paragraphs we have presented data which indicate a possible dependence of a few characteristic Coleoptera upon equally characteristic food-plants. The distribution of these beetles must depend, at least in part, upon the distribution of their food-plants which are in turn quite dependent upon daylight for photosynthesis during the growing season. Obviously, such plants are less directly dependent upon daylight for other physiological processes, and other factors are of great importance to the functioning of forest plants, e.g., moisture (Moore, '29), so that the problem is very complex.

That such food-interrelationships exist between beetles and plants is a well known fact, and the supporting literature is large. Elton ('27, pp. 57-59) states that "At whatever animal community we look, we find that it is organized in a similar way. Sometimes plants are not the immediate basis of the food cycle. This is the case with scavengers. . . . In all these cases, which are peculiar, the food supply is of course ultimately derived from plants . . ." and on page 47, "It is one of the commonest things in nature to find a herbivorous animal which is attached solely to one plant either for food, or for breeding purposes, or for both. It is hardly necessary to quote examples amongst insects, since they are so numerous." As to the degree of specificity of food-plant implied above, there is an unfortunate difference of opinion, since Shelford ('29, p. 131) notes that few phytophagous animals "are

restricted to one food plant," and finds that certain species, as the tarnished plant bug, feed on all sorts of "herbage growing in sunlight. . . . Evidently their distribution is not governed by food." The study of such generalized feeders has not been considered here, as none were observed in connection with the upland forest sere. Without doubt, some beetles would enter this category, and possibly are more common in the marginal zones of forests than they are usually considered to be. In such cases daylight may very well be more important than food in determining distribution. Other factors undoubtedly enter to the extent that final solution of the distribution problems lies in future experimentation.

Regardless of the specificity of food-plant, food is certainly of great importance in the ecology of forest Coleoptera. Shelford ('29, p. 132) mentions that "If one makes a list of the food plants of an insect in its original climatic conditions he usually finds that they are some of the predominant trees or other plants of some plant association." This view is in line with what has been said in the preceding pages, and tends to emphasize the parallel between the upland forest sere of the Chicago area, and the beetle communities involved (Park, '30).

Such an interdependence between a species and its food led to the development of the Hopkins' "Host Selection Principle" (Walsh, 1864, 1865) which has recently been confirmed by F. C. Craighead ('22, '23) and criticized by Larson ('27). Chapman ('20, p. 179) expresses his opinion that "herbivorous beetles which are dependent upon growing plant tissue for their food may be said to have the factors of food and climatic conditions more or less merged into one. Conditions which favor the growth of plants favor the food supply, and thus the growth and development of the beetles." I find this point of view suggestive since it makes for an indirect, but definite, correlation between light and the beetle communities of a forest sere. Again, Leng ('13, p. 85) suggests that food supply and shelter may be more important than the divisions used to classify plants with respect to their environment, and that (p. 163) "food for beetles constituted a more important factor than moisture"; and Hatch ('25) has seen fit to classify Coleoptera for ecological purposes, in great part on the basis of food-habits.

Shelter Relations

A discussion of shelter, as such, is difficult since the problem is interrelated inevitably with food and feeding behavior at certain seasons of the year, with breeding ranges at other times, and with hibernation and estivation. For these reasons, only the more obvious conditions of shelter will be touched upon, especially those surrounding the habitat niche of a species. That there is some niche preference operating is apparent from the condensed Tables II and III.

The figures in Tables II and III show that about one-third of the species of beetles of a forest community occur most frequently on or in the floor stratum, and are subject therefore to the intensity of daylight penetrating

TABLE II. *Species summary on niche preference*

Community	Floor	Foliage	Dead wood	Dung	Carrion	Fungus	Totals
Cottonwood.....	18	34	1	1			54
Conifer.....	9	2	13				24
Black oak.....	88	128	50	3	10	2	281
Sub-climax.....	84	94	48	1	3	2	232
Climax.....	75	42	60	8	7	45	237

TABLE III. *Species niche preference in percentages*

Community	Floor	Foliage	Dead wood	Fungus
Cottonwood.....	33.00%	62.90%	1.80%	
Conifer.....	37.50	8.30	54.00	
Black oak.....	31.30	45.50	17.70	00.71%
Climax.....	31.60	17.70	25.30	18.90

through the forest canopy and falling on the floor, or to the environmental changes consequent upon such penetration.

From an examination of the species in Table III, we find that there is indirect evidence that the kind and amount of available shelter increases with increase in mesophytism of the forest, probably reaching a height in the sub-climax forest, a conclusion reached by Shelford ('13, p. 247) for animals in general in forest succession.

It is further seen that the climax association is the most evenly balanced with respect to the inhabiting of niches on the floor, the foliage, dead wood and fungi, a conclusion in accord with what we know of the stability of the climax forest. This association, further, holds the large majority of mycetaphagous species.

The cottonwood community, as would be expected, shows relatively a high proportion of foliage forms due to the paucity of suitable dead wood. This latter is scarce since the floor is subject to burial by wind-driven sand, noted previously by Cowles ('01); and in general the deciduous communities studied show a preponderance of species taken on living plant tissue.

Weiss ('22, p. 165) finds that 26 per cent of insects in general are phytophagous, 44 per cent saprophagous and 27 per cent predaceous. Weiss and West ('22, p. 189) found that "in woods about 37 per cent of the species were phytophagous, about 35 per cent saprophagous, and this percentage appears reasonable in view of the dead timber and moist conditions; 20 per cent consisted of predaceous species . . .," and finally Weiss ('24b, p. 106) notes that "the ratio between the various types of insect food habits . . . vary in accordance with the type of vegetation," so that our data on niche preference appears to conform in general with that reported by other workers.

Coleoptera Associated with Fungi in the Chicago Area

It is the purpose here to present some of the data collected on those beetles inhabiting or feeding on fungi in the Chicago area in an attempt to show a further correlation between the succession of beetles and their distribution with associated food and shelter plants.³

It is well known that fungi are intimately associated with communities of higher plants, as well as with physical and chemical environmental factors. The nature of this association, and the degree of complexity involved are little understood (cf. Moffatt, '09, I, p. 13), although Graham ('27) found seral or ecological and seasonal succession of species of fungi (Basidiomycetes) in accord with, and related to, similar succession in the upland forest sere of the Chicago area. In general the fungi are saprophytes which serve as a link between their beetle inhabitants and the forest as a whole.

Considering fungi as habitats, the following forms may be mentioned with reference to their beetle inhabitants:

AGARICACEAE

Pleurotus ostreatus Fr.

Moffat ('09, p. 49) finds this species "occasionally throughout our district, chiefly after rains in autumn, on various deciduous trees. The erotylids, *Triplax thoracica* Say and *T. flavicollis* Lec. were taken under the bark of a red oak log which had fallen on the moist floor of a typically mesophytic white oak-red oak-elm sub-climax forest on the bluffs of the Sangamon river, near Springfield, Illinois, on April 25, 1926. Some 2 months later (July 1, 1926), these 2 species were again encountered together, this time in a large *P. ostreatus* attached to a dead limb of a sugar maple, again on the rich floor of the Joliet, Illinois, maple climax. There were 14 *T. thoracica* and 6 *T. flavicollis* in burrows or in small, rounded cavities on the gilled under surface. The burrows ramified through the body of the fungus, and extended well into the stem.

Weiss ('20a) found both of these erotylids associated with this species of fungus, in addition to other Coleoptera, giving the range of *ostreatus* from the spring to the late autumn, and its habitat as the limbs and branches of both living and dead trees.

Bulgaria inqunna.

The nitidulid, *Pallodes silaceus* Er. was taken on July 14, 1926, in an excavated cavity on the under surface of this fungus, the latter taken from the rich floor of the young beech-maple climax near Michigan City, Indiana.

POLYPORACEAE

The woody "shelf" or "bracket" fungi, represented by *Polyporus*, hold a different fauna usually than the agarics, and occupy a more extensive position in the upland forest sere, being found through the pioneer as well as through the climax communities. The firmer texture of these fungi is at once more resistant to ravages by beetles and consequently far more stable than the softer, fleshy forms. With this comes the persistence through a number of seasons, and the opportunity for seasonal succession and a more permanent tunneling of the tissues, hence a protected and relatively constant habitat. Weiss ('20c) has given a general account of the insect enemies of polyporoid fungi. The following data are presented from my records of woody species in the immediate vicinity of Chicago.

³ I am indebted to Dr. V. O. Graham for the determination of the fungi.

***Polystictus cinnabarinus* Jacq.**

This fungus was found on a black oak log, on the floor of the pioneer black oak community at Dune Park, Indiana, on April 4, 1927. The specimen held 2 *Hoplocephala bicornis* (Fab.), 1 male and 1 female.

***Polyporus* species.**

A number of species of *Polyporus* have been found associated with various Coleoptera, and the fungi are at present pending determination. The beetle fauna may be mentioned as follows:

Phenolla grossa (Fab.). Five were taken May 28, 1927, with *Diaperis* mentioned later. Weiss ('20b) found *P. grossa* feeding on *Polyporus versicolor*, and ('24a) found it associated with *P. sulphureus* on July 9 (Iowa).

Megalodacne heros Say. Taken beneath the bark of elm in a sub-climax forest, near a clump of *Polyporus* at Glenview, Illinois (April 10, 1927). I have taken this species feeding on *Polyporus* on dead chestnut logs, in burrows it was excavating on the underside, in the rich tulip-chestnut climax at Montreat, North Carolina (July 13, 1928). *M. heros* has also been sent to me from Soldier's Grove, Wisconsin (July 13, 1928), where it was feeding on *Polyporus* in one instance, and, in other specimens, was apparently going into hibernation in the burrows of the fungus. Thus *M. heros* is of wide distribution, as is indicated by Leng ('20), although not common in the Chicago area. Dury (1878) says of *Microsternus ulkei* (Cr.), a related erotylid, that it feeds on "polyporae" growing on logs: "The habits of the adult (p. 211) differ somewhat from *M. heros* and *fasciata*, in that *Meg. ulkei* lives more inside the fungus and is less inclined to drop to the ground when the fungus is jarred," the species being recorded by Dury from Kentucky in July. Weiss ('20b) found the related *M. fasciata* (Say) in *Polyporus versicolor* L.

Boletotherus cornutus (Panz.), both sexes, were taken in *Polyporus* September 11, 1928, from a log on the wet floor of the sub-climax Coffee Creek flood-plain near Chesterton, Indiana. It was also taken June 1, 1929, under the same conditions at the same community, and under the same conditions from the maple climax at Joliet, Illinois, on July 1, 1926. *B. cornutus* occurs through the rich forests, hibernating beneath bark of logs on the floor or in polyporoid fungi (November 15, 1929, in the beech-maple climax at Hiram, Ohio) or feeding on *Polyporus* tissues (Volo, Illinois, August 15, 1926). It may be present in such numbers as to be the dominant species of the fungus community, 4 males and 14 females having been taken from one *Polyporus* at Montreat, North Carolina, with *Megalodacne heros* mentioned previously. Whether its distribution is a consequence of the distribution of its food-plants, or of certain physical factors, such as light and moisture, or both, is not known. Weiss and West ('20) found the small, oval egg capsules of the related *B. bifurcus* Fab. on the upper surface of a related fungus, *Fomes applanatus* in New Jersey on August 4. The larvae, when hatched, bored directly into the tissues of the fungus, and the egg capsules subsequently weathered away. Weiss ('20b) found *B. bifurcus* feeding on *Polyporus versicolor*.

Diaperis maculata Oliv. Fifteen specimens were taken from fresh excavations in *Polyporus* on May 28, 1927, in a sub-climax oak-elm-hickory forest and Weiss ('24a) found this species on *Polyporus spraguei* in Iowa in July. Much data could be added on *D. maculata*, since it also occurs in many communities, and often in such numbers as to be the dominant species of the fungus habitat involved. As in *Boletotherus*, it may hibernate in numbers either under bark or in burrows in fungi.

Hoplocephala bicornis (Fab.) was taken from May 19 to May 30 in numbers from cells and galleries in *Polyporus*, both in sub-climax and climax forests. Some were kept in the fungi from May 19, 1927, to November 1, 1927, at laboratory temperatures in the dry, woody tissues. Weiss ('20b) found this species also on *Polyporus versicolor*.

Synstrophus repandus (Horn). Five taken May 28, 1927, with *Diaperis* mentioned above.

Ceracis sallei Mel. Fifteen taken on April 20, 1927, from burrows in old, dry *Polyporus* in the pioneer black oak community at Dune Park, Indiana.

Osmoderma cremicolor Knoch. taken on the under side of a fresh *Polyporus* in a sub-climax oak community, August 15, 1926; the species has been taken under similar conditions in the tulip-chestnut climax at Montreat, North Carolina.

Fomes lobatus, a polyporoid related to *Polyporus*, was found on the climax maple floor at Joliet, Illinois, on April 18, 1927. The fungus held a number of beetles which may be mentioned briefly: *Philonthus blandus* Grav., 2; *Tachinus pallipes* Grav., 10; *Baryodma sculptiventris* Casey, 1; *Hister marginicollis* Lec., 6. From their actions, these last might have been feeding on the fungus juices. There were also: *Osmosita colon* Linn., 1; *Glischrocheilus fasciatus* Oliv., 3; *Tomarus pulchellus* Lec., 1; *Pisenus humeralis* Kirby, 36, the most abundant species.

HYDNACEAE

The following account is dealt with in more detail since it (1) represents a thriving mycetocolous community, (2) presents certain features of seasonal succession, (3) and describes the fauna of a little observed fungus.

Hydnum septentrionale.

Two specimens of this interesting fungus were observed. The first (A), about 1 square foot in area, came from the moist floor of the climax maple association at Joliet, Illinois, on July 1, 1926. The tissues were soft, and as much as 3 inches thick in places. The entire fungus was brought to the laboratory.

On April 12, 1927, another specimen of *Hydnum* was taken from the base of a large sugar maple (*Acer saccharum*) from which it had probably fallen. This second specimen (B) was left *in situ* for future examination. In size and condition it was practically identical with the first specimen, and was found in the same spot. The drier portions were found to be the most thickly populated by animals, and the specimen probably held, in addition to its normal inhabitants, some species which were using the fungus as a hibernaculum.

The following record of the examination of specimen (B) at successive intervals shows the progressive decomposition of *Hydnum* over a period of more than 2 years: April 12, 1927, soft, fresh, area 1 sq. ft., wt. 2.5 pounds; May 2, 1927, condition approximately as on April 12; June 2, 1927, slightly drier and smaller through shrinkage from loss of water, lighter; April 25, 1928, decidedly drier and smaller, edges becoming worn and split; May 23, 1928, progressively drier and lighter in weight; June 14, 1928, one-fifth its former size on April 12, 1927, dry save for a few covered areas; June 30, 1929, area 3 sq. in., wt. 0.5 pound.

Table IV lists the Coleoptera taken in *Hydnum* with respect to time of year, the fungus being defaunated of adults as far as possible on each trip. The numbers in the table show the number of species taken.

We see from Table IV that 36 species, divided among 10 families of Coleoptera, frequent this fungus and make up the dominant part of the community. Neglecting the first specimen of *Hydnum* (A), since it was brought into the laboratory, and considering the second (B), which was allowed to remain in the field, two features are of interest:

1. There is an indication of community or seral succession from April 12, 1927, when the fungus was apparently fresh, to June 14, 1928, the last visit on June 30, 1929, being separated for special consideration. During this period of a year and 2 months the fauna fluctuated with the change in condi-

TABLE IV. Seasonal occurrence of Coleoptera in a specimen of *Hydnum septentrionale*

Species	1926	1927			1928		
	July 1	April 12	May 2	June 2	April 25	May 23	June 14
Carabidae							
<i>Lebia ornata</i> Say						I	
Silphidae							
<i>Ptomophagus pusio</i> Lec.		4					
<i>Agathidium oniscoides</i> Beauv.	3						
<i>A. politum</i> Lec.	I	I					
Staphylinidae							
<i>Stilicus dentatus</i> Say	I						
<i>Philonthus cyanipennis</i> Fab.	3						
<i>P. blandus</i> Grav.	5		3	3		I	
<i>Staphylinus maculosus</i> Grav.							I
<i>Ontholestes cingulatus</i> Grav.					I	I	
<i>Quedius capucinus</i> Grav.	9						
<i>Tachinus pallipes</i> Grav.	7	5			20	6	I
Histeridae							
<i>Hister harrisi</i> Kirby						I	
<i>H. marginicollis</i> Lec.	16		2	I	I	4	
<i>H. abbreviatus</i> Fab.						I	
Nitidulidae							
<i>Osmosita colon</i> Linn.		10	16				
<i>Epuraea rufa</i> Say		5					
<i>Glischrocheilus fasciatus</i> Oliv.	2	2			34		I
<i>Stelidota octomaculata</i> Say	12						
Cryptophagidae							
<i>Tomarus pulchellus</i> Lec.		I	65*	10		I	I
<i>Crosimus hirtus</i> Casey			4				
<i>Glyptophorus mycetoecus</i> Park †			3				
<i>Cryptophagus acutangulus</i> Gyll.		I	I				
<i>C. nodangulus</i> Zimm.		9	10				
<i>Henoticus serratus</i> Gyll.			I				
<i>Anchicera epphiata</i> Zimm.			10				
<i>A. pusio</i> Payk.			3				
<i>A. ovalis</i> Casey		12*	4				
Mycetophagidae							
<i>Mycetophagus flexuosus</i> Say	I		38	4		22	27
<i>M. pluripunctatus</i> Lec.		2					
Tenebrionidae							
<i>Diaperis maculata</i> Oliv.				I		18	8
<i>Platydema ruficorne</i> Sturm.			2			4	
<i>P. americana</i> C. and B.							
Melandryidae							
<i>Pisenus humeralis</i> Kirby			4	3		3	2
Scarabaeidae							
<i>Aphodius distinctus</i> Mull.		I					
<i>Ataenius cognatus</i> Lec.				I			
<i>Geotrupes splendidus</i> Fab.	I						
Chrysomelidae							
<i>Lina lapponica</i> Linn.				**			

* Copulating.

** Elytral fragments.

† Type locality (Park, '29a).

tion and composition of the fungus. Both the change in season, as such, bringing with it changes in the environmental factors, as well as organic change of the fungus itself, are involved. Such ecological succession is found in both the total number of specimens collected on each date, and in the total number of species as shown in figure 1.

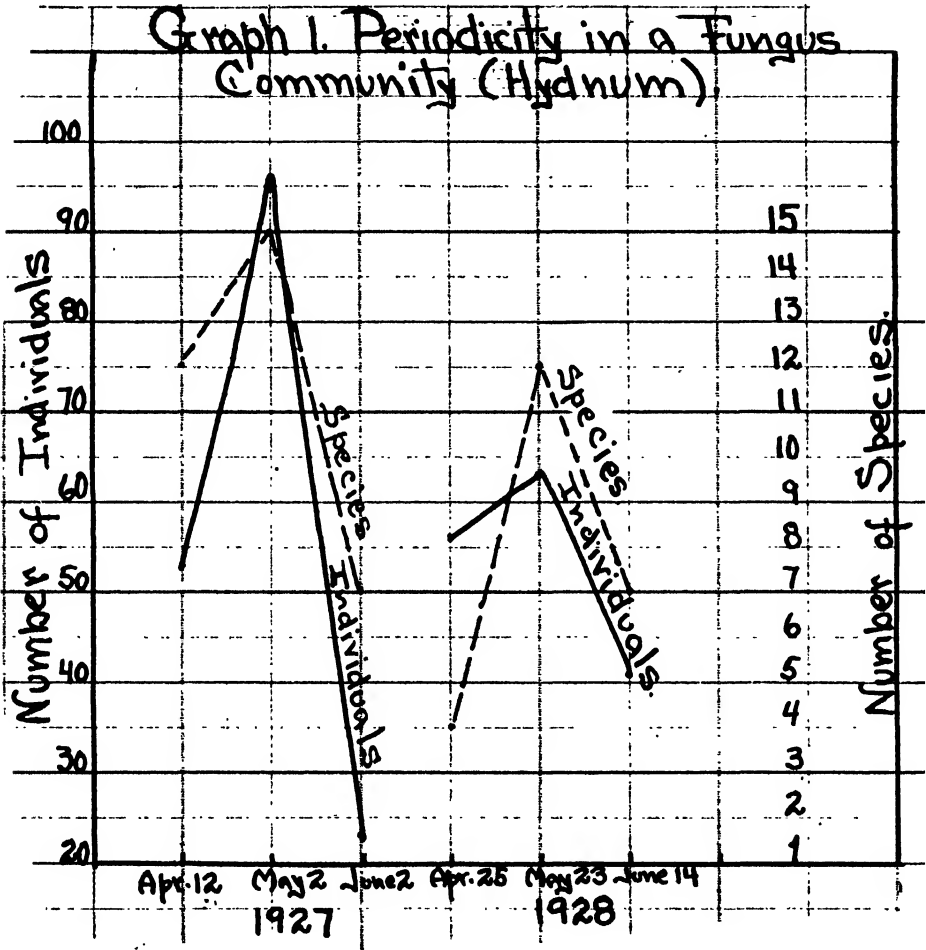


FIG. 1. Graph showing the periodicity of Coleoptera, species and individuals, in a fungus (*Hydnum septentrionale*).

Each spring the fungus community holds a number of species which are characteristic for such a community, as well as hibernants using the fungus over the winter. As the mycetophagous larvae pupate, a peak in numbers of both individuals and species occurs in May, the increase being an approximate doubling over the April totals. During this time the fungus is moistened by spring rains, and as the season advances into June, there is a falling off in the

population which apparently parallels the gradual drying, cracking and shrinking of the fungus through loss of liquids. Where such a fungus as *Hydnum septentrionale* is used, this seasonal cycle is modified progressively through time, and the rhythm or periodicity is more or less changed the second and third years, as would be expected. With such fungi as *Polyporus* and related genera, the firmer tissues would be more resistant, and the rhythm might possibly be more constant.

In the drier portions of the fungus certain families, e.g., the Tenebrionidae, are more numerous, as has been previously noticed by Weiss. Other families, e.g., Staphylinidae and Cryptophagidae, are usually more common in the moister areas, while the very moist portions are apparently not as productive as the dryer sections. Thus within the fungus, per se, as in the forest community as a whole, stratification may occur.

2. Another point is interesting. Figure 1 shows seasonal as well as seral succession. This is indicated by a study of species distribution in terms of total species and individuals per month, regardless of age of fungus (Table V).

TABLE V. Seasonal distribution of species in *Hydnum*

Month	Individuals (imagines)	Species
April	109	16
May	159	27
June	64	14

Just how much of this periodicity is a consequence of change in the fungus, and how much is due to seasonal change, apart from the effect on the fungus, is not certainly known at present. It is interesting, however, to note that, as with the upland forest sere as a whole (Park, '29b, '30), the maximum number of species occurs in May.

Mounding of Fungi

There is another point at which ecological changes within the fungus community parallel similar events taking place in the forest community as a whole.

The same specimen of *Hydnum septentrionale* (B) was visited approximately one year later (June 30, 1929), and was found almost wholly decayed but still soft and moist in spots. The tissues remaining weighed about half a pound, that is, one-fifth of the original weight, and the fungus measured roughly 3 square inches in area.

With these changes in condition, there was an interesting change in the fauna. In addition to the regular mycetocoles, e.g., Phalacridae, 8 *Hister marginicollis* Lec., 1 *Philonthus cyanipennis* (Fab.), and 5 *Tachinus pallipes* Grav., other species were making their appearance. Among the latter may be mentioned the mycetaeid, *Rhanis unicolor* (Zieg.), which is taken regularly in the Chicago area beneath bark of logs in the soft sapwood from stages 2 to 4 and in moist, mounding logs in stage 5 of the log succession; the staphylinid,

Paederus littorarius Grav., usually found along the moist margins of streams, ponds, and of marshes; the widely distributed snail, *Anguispira alternata* (Say) (*Pyramidula auct.*) which is taken under bark of logs on the forest floor, regularly in many decaying fungi, on the moist floor of rich woods, et cetera; millipeds (Polydesmidae); phalangids (*Leiobunum*); and an ant (*Leptothorax*).

The snails, millipeds, phalangids, and ants were also present in abundance on the adjacent forest floor. The *Leptothorax* were numerous on both fungus and the neighboring soil, and were actively carrying off staphylinid larvae from the former, and spiders, culicids, polydesmids, and tipulids from the latter.

Ecologically, the fungus had become practically equivalent to the forest floor, and was in the mounding condition so that it would seem that fungi pass through a definite series of changes which parallel stages in the well known log succession.

Seral Succession of Mycetocolous Coleoptera

In addition to their distribution by species of fungus, and to the seasonal succession in the more resistant specimens, the mycetocolous species of Coleoptera in the Chicago area may be arranged on a seral basis as will be seen in Table VI. Apparently the general factors controlling the distribution of beetle inhabitants of fungi are not necessarily different in their major aspects from those controlling the species of the upland forest sere as a whole.

Behavior of the Mycetocolous

The behavior of these various species is different, as would be expected. Thus, briefly, the tenebrionids feed on the drier portions of fungus tissue, and the cryptophagids, et cetera, on the softer areas. Certain forms, as *Lina lapponica*, use the fungus as a hibernaculum, and this species, with others, regularly frequent the climax floor for hibernation (Park, '30). The same may be said for such forms as *Lebia ornata* and the coprocolous scarabaeids; and the former, with many other species, may possibly represent accidental or stray residents from other communities. The scarabaeids noted, however, may actually feed upon the fungus tissues, or even carrion, in addition to their normal food.

The staphylinids are largely carnivorous,⁴ and probably attack the mycetophagous herbivores in their several developmental stages (Davis, '15), but some species may feed upon the fungus tissue, as for example *Tachinus palipes*.

The silphids and histerids may either devour the fungus, or prey upon the

⁴I have observed, on 3 occasions, in Sayner, Wisconsin, the staphylinid *Creophilus villosus* (Grav.) to snap up, run away with, and subsequently devour dipterous larvae in experiments with fish carrion. This has been observed in the field with other species, e.g., *Staphylinus*, and *C. villosus* has been experimentally fed on larvae and pupae of *Tribolium* in experiments to be reported later.

TABLE VI. *Seral succession of Mycetocolous Coleoptera in the Chicago area*

Species	Pioneers black oak	Subclimax	Climax
<i>Ceracis sallei</i> Mel.	×		
<i>Phenolla grossa</i> Fab.		×	
<i>Megalodacne heros</i> Say		×	
<i>Boletotherus cornutus</i> Panz.		×	
<i>Snystrophus repandus</i> Horn.		×	
<i>Osmoderma eremicolor</i> Knoch		×	
<i>Hoplocephala bicornis</i> Fab.	×	×	×
<i>Diaperis maculata</i> Oliv.		×	×
<i>Triplax thoractica</i> Say		×	×
<i>T. flavicollis</i> Lec.		×	×
<i>Pallodes silaceus</i> Er.			×
<i>Philonthus blandus</i> Grav.			×
<i>Tachinus pallipes</i> Grav.			×
<i>Baryodma sculptiventris</i> Casey			×
<i>Hister marginicollis</i> Lec.			×
<i>Osmosia colon</i> Linn.			×
<i>Glischrocheilus fasciatus</i> Oliv.			×
<i>Tomarus pulchellus</i> Lec.			×
<i>Pisenus humeralis</i> Kirby			×
<i>Plomophagus pusio</i> Lec.			×
<i>Agathidium oniscoides</i> Beauv.			×
<i>A. politum</i> Lec.			×
<i>Philonthus cyanipennis</i> Fab.			×
<i>Staphylinus maculosus</i> Grav.			×
<i>Ontholestes cingulatus</i> Grav.			×
<i>Quedius capucinus</i> Grav.			×
<i>Hister harrisi</i> Kirby			×
<i>H. abbreviatus</i> Fab.			×
<i>Epuraea rufa</i> Say			×
<i>Stelidota octomaculata</i> Say			×
<i>Crosimus hirtus</i> Casey			×
<i>Glyptophorus mycetoeus</i> Park.			×
<i>Cryptophagus acutangulus</i> Gyll.			×
<i>C. nodangulus</i> Zimm.			×
<i>Henoticus serratus</i> Gyll.			×
<i>Anchicera epphipiata</i> Zimm.			×
<i>A. pusilla</i> Payk.			×
<i>A. ovalis</i> Casey			×
<i>Mycetophagus flexuosus</i> Say			×
<i>M. pluripunctatus</i> Lec.			×
<i>Platyedema ruficorne</i> Sturm.			×
<i>P. americana</i> C. and B.			×

mycetophagous larvae, or both, as their feeding habits are open to some question, contrary to the general opinion some years ago; and recent work tends to show these forms, e.g. *Necrophorus* and *Silpha*, as eating dipterous larvae as well as carrion, or only the former (Clark, 1895; Dury, '06; Selous, '11; Steele, '27; Davis, '15), and several species of *Hister* have been shown to have predaceous habits, at least in part (Davis, '04).

It is even possible that the histerids taken were subsisting on the fungus juices in large part, since Jaques ('15) has suggested that the genus *Saprinus* feeds on the juices of carrion, rather than the carrion, per se, or the contained maggots.

The survey of these data, preliminary in character, convince one of the

complex ecology within such a limited community as that of a fungus. One sees here a picture in miniature of many of the relations existing in the forest community as a whole; of the presence of seral and seasonal succession; of narrowly limited and wide ranging forms.

It should be remembered that factors affecting the distribution of fungi, such as illumination, temperature, humidity, soil and the species of trees present, would indirectly affect the distribution of the beetle inhabitants.

Summary

The effect of light upon the forest Coleoptera may be considered in at least 2 ways, the direct effect of light, and its indirect effect through modification of other factors, both physical and biological.

It is clearly recognized that intensity of illumination is but one of many such indirect factors that may be involved. Data are presented to show that daylight may act indirectly through its influence on food and shelter plants to affect the distribution and activity of beetles within a forest sere, and food-plants apparently are especially important in determining beetle distribution.

Seral communities of beetles can be recognized which are associated both with autotrophic and saprophytic plants. It is shown that the fungus community parallels the greater forest community of which it is a part, both in seral and seasonal succession, and in passing through stages in decay similar to those shown by logs on the forest floor.

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PLANT SOCIOLOGY AND VEGETATIONAL CHANGE
ON
HIGH HILL, LONG ISLAND, NEW YORK¹

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Introduction

HISTORICAL SKETCHES AND MORE IMPORTANT PAPERS

The grasslands of *Andropogon scoparius*² on Long Island occur in more or less restricted but definitely marked regions of the Island, namely, Hempstead Plains, Montauk, Shinnecock Hills, and portions of West Hills of which High Hill, the subject of this study, is a part. Harper ('12, p. 262) says that the Hempstead Plains, in the central portion of Nassau County, Long Island, are a bit of prairie similar to parts of the Great Plains in the central United States. The absence of trees on these plains he attributes chiefly to recurring fires. Taylor ('23, p. 24), recording the results of a comprehensive study of the vegetation of Montauk, states that the Downs show infinite gradation between grassland and the attempt to produce some sort of woody vegetation. He likewise studied the vegetation of the "kettle holes" in that region, and found gradations between "kettle holes" that have no trees or shrubs (grassland) and those that exhibit a forest or climax condition. He concludes that the Downs appear to be incapable of producing a forest except with protection from the wind. He says, "Indeed, the wind is so terrific, of such long-continued gale force, that . . . one is apt to think the wind is the only factor controlling the present distribution of vegetation" at Montauk (p. 57).³

¹ Immediate publication made possible by Mr. Robert W. De Forest, through a gift to the Biological Laboratories, Cold Spring Harbor.

² Plant names are according to Gray's Manual, 7th Edition, and Grout's "Mosses with Hand Lens and Microscope."

³ For the opportunity of studying the vegetation of this very interesting locality the author is indebted to Mr. Robert De Forrest on whose estate High Hill is situated, and who has also given valuable information concerning it. With a fine public spirit, High Hill and the adjoining woods are kept open to all who are interested in science and art.

Thanks are due to the Long Island Biological Laboratory: to Dr. R. G. Harris, Director, for the use of the facilities of the Laboratories and the Library; and to Doctor H. S. Conard, botanist, for valuable assistance and helpful suggestions.

It is a pleasure to express appreciation for the aid rendered by the following students at the Biological Laboratory: to Mr. Herbert Schmidt in the preliminary study of the vegetation; to Miss Beth Burgess for the one meter quadrat of the grasslands; and especially to Ethel Lewes Blizzard for making the retracings from the original chart quadrats.

The grasslands of the Shinnecock Hills undoubtedly would support a growth of shrubs and trees if the biotic factors were removed.

On High Hill, the grassland is being invaded by a deciduous forest. Whether this bit of vegetation is a fragmentary community is questionable. It is the opinion of the writer that it should be classed as a subclimax formation, as the following remarks indicate.

First, the older inhabitants of the vicinity of West Hills think that at one time or other the whole region was brought under cultivation. It is possible, however, that the crown of the hill served only for grazing. In this connection, a statement of Spooner (Pelldreau, 1898, p. 18) concerning Silas Wood, one of the earliest historians of Long Island who was born in 1769 in West Hills, is of interest. He says "From a high point near his (Wood's) residence at West Hills, he had often looked upon the Sound (northward) and the blue line of the mainland beyond on one side and the broad Atlantic Ocean on the other. When he came to hear Hempstead Harbor Hill . . . was claimed as the highest ground on the Island, he felt assured that a point at West Hills was higher. This is a spot known as 'Oakley's high hill field.' . . . In 1825, Wood had the hill surveyed, and after determining the elevation from sea level showed that High Hill is higher than Harbor Hill. This position of vantage to his native hills was evidently gratifying to Mr. Wood, for in 1832 he took the pains to have the field notes of his survey with his name, entered on the records of the town by pasting the same firmly in the book of the town meeting."

The shoulders of the hill were at that time cleared of trees, and the acreage of grassland was therefore greater than now. For this reason an unobstructed view of the Sound was obtained. It is reasonable to infer that the statement "High Hill Field" had reference to grassland existing as such in 1825; how much longer, no one knows.

Secondly, according to Wood (Pelldreau, 1898, p. 23), the forests were burned annually by the Indians and later the trees were cut by the colonists, which would make it possible for grass to grow more readily. He says, "By neglecting the Indian practice of annual burnings, in a few years the young timber and underbrush increased so as to injure the feed in the woods. . . . In 1667, the town court appointed two men to warn the inhabitants to meet, to fire the woods at such time as they should think fit."

Thirdly, according to Prime (1845, p. 19), still another factor aided in depleting the forest, as follows: "Previously to the introduction of anthracite coal into general use, a large portion of the supply of fuel in the city of New York, . . . thousands of cords not only of pine from the sandy lands but of oak and hickory of the finest quality from the more elevated parts, were transported to that market . . . and singular as the fact may appear, there is probably no district of the country where a tract of land, cut entirely smooth, is replaced by natural growth with more rapidity than on the rough and elevated parts of this Island."

Fourthly, after the Revolutionary War, agriculture was brought to a high state of development. According to Mr. Henry Hicks (Unpubl., 1924), the Long Island farmer was prosperous from about 1790 to 1850. During this time, parts of the wooded interior were cleared merely for the timber again and again; grain crops, cattle, sheep, dairy products, firewood and timber constituted the chief produce of the farms.

From the above statements, it seems clear that the forests of the higher and more rugged portions of the Island had been "cleared" of trees, possibly several times. It is equally evident that the plants of the grassland established an equilibrium such that they were able to repel invasion for a long period of time.

At present, great portions of the Island, as at High Hill, are held in severalty by private owners who foster the growth of native vegetation.

THE PROBLEM

High Hill is situated in Suffolk County, Long Island, in latitude $40^{\circ} 39''$ N., longitude $73^{\circ} 26''$ W., at an elevation of 420 feet above sea level. It is about 7 miles inland from the northern coast of the Island. Because of its situation, it is protected from the devastating effects of high wind; and its position as part of a large estate practically eliminates the danger of fire destroying the vegetation. Possibly on account of the absence of these two major eliminating factors, and also partly due to the mesic condition of the soil, the forest has marched boldly over the shoulders of the hill, and is now invading the grassland.

Because of the peculiar social relation of the plant communities on High Hill, and the splendid opportunity which the locality affords for the study of various species as dynamic-genetic factors in plant sociology, this work was undertaken.

Physiographic Features

The physiographic features of the Island are simple. In common with all of northeastern North America, the northern part of the region now occupied by Long Island was invaded in recent geological time by great continental glaciers. The great ice sheets moved southward across New England and New York, eroding the land surface, carrying materials of all grades of coarseness, and finally depositing sand, gravel, loam, and rock throughout their entire courses. Such deposits usually attain their greatest thickness along the front of the ice. As the ice front fluctuates backward and forward over large or small distances, a series of terminal-moraine deposits may be formed. The two ranges of hills found on Long Island are terminal moraines (Bonsteel ('03)). Of these, the southern is the older and extends from Bay Ridge northeasterly to Roslyn, thence continuing to Montauk Point in a series of elevations. The more important of these elevations are West, Dix, Comac, Bald, and Shinnecock Hills (Merrill (1884)). High Hill is a portion of West Hills.

High Hill consists of gravel and sand, more or less stratified. It is no doubt rather similar in structure to the section exposed at Crossman's brick yard in Huntington, which according to Merrill (1884) shows the following composition:

Till and stratified drift	10 ft.
Quartz gravel	45 ft.
Red and blue loam or sandy clay	20 ft.
Diatomaceous earth	3 ft.
Red plastic clay	20 ft.
Brown plastic clay	25 ft.

The surface soil as it exists today on High Hill has been described by Bonsteel ('03) as being composed of Norfolk gravel which consists of rounded quartz gravel from .5 inch to 5-6 inches in diameter, mixed with a small amount of iron-stained quartz sand resting upon the sticky Cretaceous clays. Agriculturally the Norfolk gravel is almost useless. As regards the climatic conditions, the reader is referred to the paper by Taylor ('23) who gives them adequate treatment.

The Grassland (*Andropogonetum scoparii*)

The *Andropogonetum scoparii* on High Hill is a stage in a secondary succession, in the sense of Clements ('16, p. 60). Because of the xeric condition of the soil on top of the hill, and the probability that the colonists—possibly the Indians, too—had used it exclusively as pasturage, it seems likely that the grass association followed immediately the destruction of the mesic deciduous climax forest. As is well known, Long Island is situated in the general forest area of northeastern North America. It is not likely that any of the virgin forest exists as such in Suffolk County today. The trees growing on the various slopes of High Hill are "lineal descendants of the primitive woods" and without any reasonable doubt represent many of the species which inhabited them in the original or virgin condition (except the chestnut tree, *Castanea dentata*, which has been destroyed by the fungus, *Endothia parasitica*).

The *Andropogonetum scoparii* is a two-layered community (top and root) with competition in the root layer only. The paucity of species in this unit of vegetation is striking when compared with the number reported by Taylor ('23) in the Downs at Montauk and by Harper ('12) on the Hempstead Plains. This is another bit of evidence, I think, that the grassland on High Hill is a secondary succession; that is, the ecological factors of the habitat were such as to bring about a significant selection of species from the first. In this case, the selection is the result of the burning and finally cutting out of the climax forest. It is well known that the more extreme the habitat conditions are, the more relentlessly will seedlings be weeded out.

Table I gives a list of the species of the plants found in the grassland, all being herbs except one which is a tree and considered a pioneer invader.

TABLE I. List of plants found in the grassland at High Hill, Long Island

<i>Andropogon scoparius</i>	<i>Cladonia symphyocarpa epiphylla</i>
<i>Cladonia rangiferina</i>	<i>Polytrichum piliferum</i>
<i>Polytrichum commune</i>	<i>Rubus villosus</i>
<i>Bryum coespitium</i>	<i>Carex virescens</i>
<i>Ceratodon purpureus</i>	<i>Stenophyllus capillaris</i>
<i>Hypericum gentianoides</i>	In old ashes { <i>Gnaphalium polycephalum</i>
<i>Hypericum perforatum</i>	<i>Verbascum Thapsus</i>
<i>Hieracium scabrum</i>	<i>Juniperus virginiana</i>
<i>Chrysanthemum leucanthemum</i>	Seedlings of :
<i>Sericocarpus asteroides</i>	<i>Quercus velutina</i>
<i>Juncus tenuis</i>	<i>Quercus alba</i>
<i>Solidago rugosa</i>	<i>Robinia Pseudo-Acacia</i>
<i>Rumex acetosella</i>	

It is interesting to note that *Baptisia tinctoria*, *Aletris farinosa*, and *Polygala polygama*, so common in the Hempstead Plains and in the Downs of Montauk, were not found on High Hill. Taylor ('23, p. 22) states that *Baptisia tinctoria* has been introduced in the Downs since 1898.

Andropogon scoparius, the dominant plant on the top of High Hill, occurs in clumps or tussocks. The culms (stems) grow to a height of 2 to 3 feet. The habit of this plant is well shown by the photograph (Fig. 1). Its very extensive root system which is well illustrated by Weaver and Clements ('29,



FIG. 1. One meter quadrat of grassland, showing tussocks of *Andropogon scoparius*. Photograph by Dr. H. S. Conard.

Fig. 131), may reach depths of from 2 to 5 feet in the gravel and sand, growing into a tangled and interwoven mass of fibrous roots. By this means, *Andropogon scoparius* is not only able to bind the sand and hold it against the wind, but also to form a resistant and tough turf. In this respect, sociologically, the species serves well as a consolidating force in the association.

The tussocks of *Andropogon scoparius* occur from a few inches to several feet apart, and, growing in considerable abundance in the coarse gravel and sand, in the spaces and runways between the tussocks, are the two species of

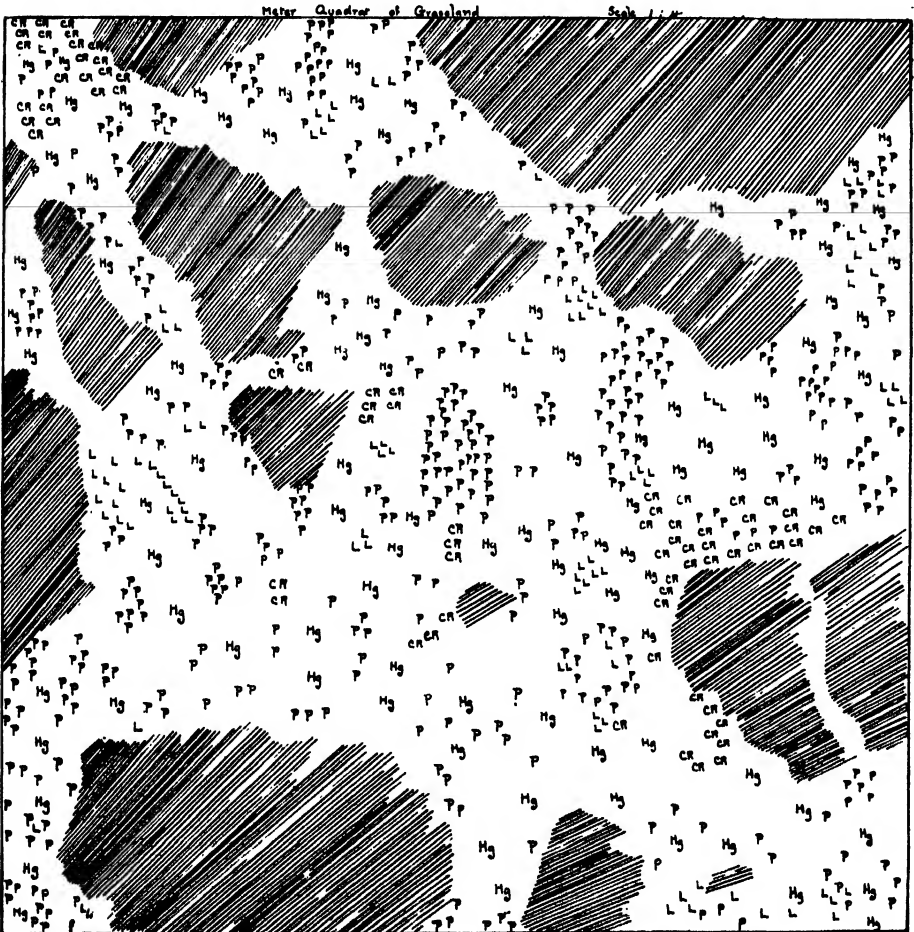


FIG. 2. One meter quadrat—grassland.

- ///// Tussocks of *Andropogon scoparius*
- CR *Cladonia rangiferina*
- Hg *Hypericum genitanoides*
- P *Polytrichum piliferum*
- L *Cladonia symphylicarpa epiphylla*

lichens and one species of moss (*Polytrichum piliferum*) mentioned above. These may be termed the primary species of the association. The one meter quadrat (Fig. 2) shows the frequency and distribution of these plants. The rest of the species named are more or less sparsely scattered in the grassland. None of them appears in sufficient abundance at any time to change the aspect of the grassland, with the possible exception of *Chrysanthemum leucanthemum*, *Hypericum gentianoides* (which appears abundantly during August but the plant itself is very small and the flower inconspicuous), and *Juniperus virginiana* (which is described below).

The bunch grass, lichens, and moss, represent a social relationship, which, by the aid of biotic factors mentioned above, has served to retard vegetational change (Cooper, '26), or succession, for at least a century and a half and probably longer. The bonds that unite this communal life may be termed commensal union, following Braun-Blanquet ('28, p. 7), from whom the following is quoted:

"According to Van Beneden, we understand by commensal organisms those which enter into competition separately, and their common relation consists in the fact that they simultaneously utilize the various life conditions of a given habitat. 'Le commensal est simplement un compagnon de table.'"

"The relation between commensals rests upon a struggle for space, light,

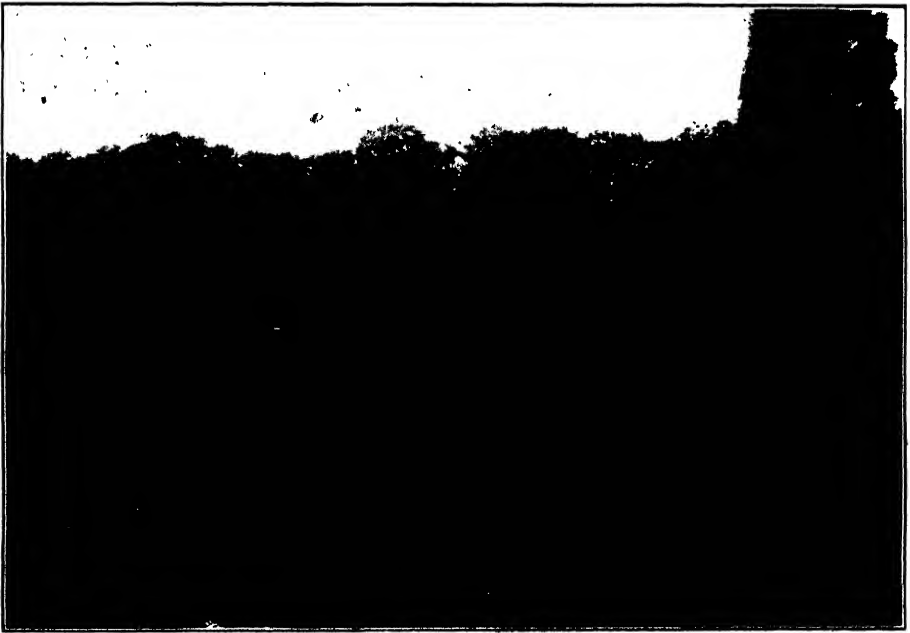


FIG. 3. A portion of the *Andropogonetum scoparii* looking westward. In the foreground, a pure stand of *Andropogon scoparius*; in the middle, clumps of *Myrica carolinensis*; in the background, the climax mixed oak forest.

and food. The struggle for existence goes on between similar commensals when different species have the same or nearly the same requirements. The struggle is most intense between individuals of one and the same species. But the table companions may have different needs, either because they use different foods, or because their organs occupy different layers of soil."

Andropogon scoparius contributes to the association protection through its dynamic quality of consolidation and stabilization. The lichens are fungus-like organisms which hold within the meshes of their hyphae an alga, from which they obtain carbohydrate nutrients manufactured by means of the chlorophyll of the algal cell. The fungus part corrodes the stones and sand by which the mineral constituents necessary for the life of the lichens are obtained. The two organisms, fungus and alga, merge into a composite and more aggressive organism, a lichen—a new organism, which is wholly self-sufficient from the stand-point of competition and has a specific ecology. The excess of inorganic salts for which the lichens are responsible leaches through the soil and aids in supplying the bunch grass with mineral nutrients.

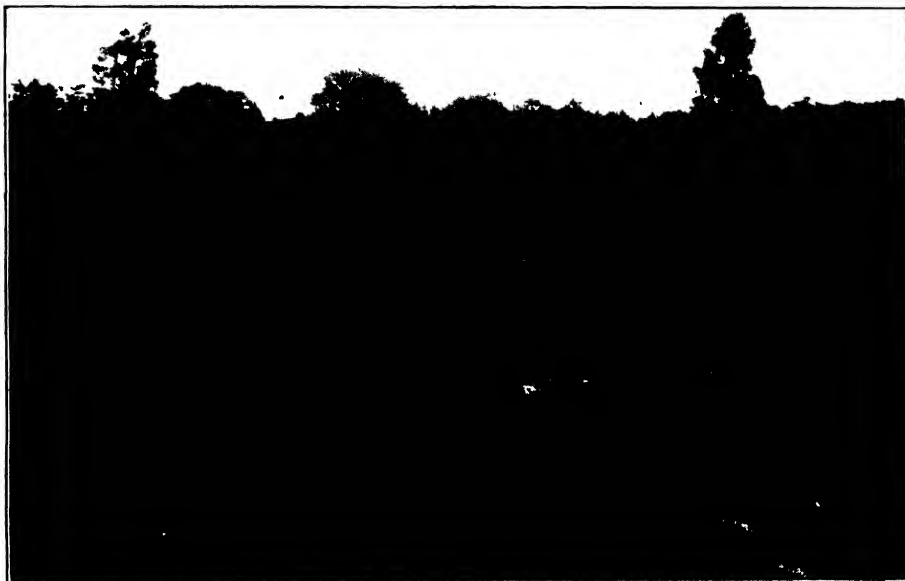


FIG. 4. A portion of the *Andropogonectum scoparii* looking eastward. A salient of shrubs to the left following the *Myrica carolinensis* into the grassland. Also, *Juniperus virginiana*. In the background, a mixed forest of *Quercus-Betula*; to the extreme right, *Robinia-Pseudo-Acacia*.

Both lichen and moss aid in soil formation. Both forms of plant are xerophytes and revive well in the presence of moisture. The secondary species which occur in the grassland do not possess dynamic-genetic potentialities of any importance, save *Juniperus virginiana*, and the oak seedlings, which are treated below.

Juniperus virginiana is the first and only tree to invade the *Andropogonetum scoparii* directly. It is to be considered a successful invader since establishment follows (see Figs. 3 and 4). The Juniper possesses the dynamic-genetic qualities of an aggressor and invader, but without any constructive or destructive value to the association. That is, it does not initiate succession of any kind, nor does it destroy vegetation to any marked degree.

The Juniper is a constant inhabitant of xeric regions throughout the eastern portion of the United States (Cowles, 1899; Harshberger, '00; Jennings, '09; Chrysler, '10; Nichols, '14).

In the minds of some people the presence of the Juniper is an indication of an abandoned field. This is true in part, but not always so. Harper ('12)

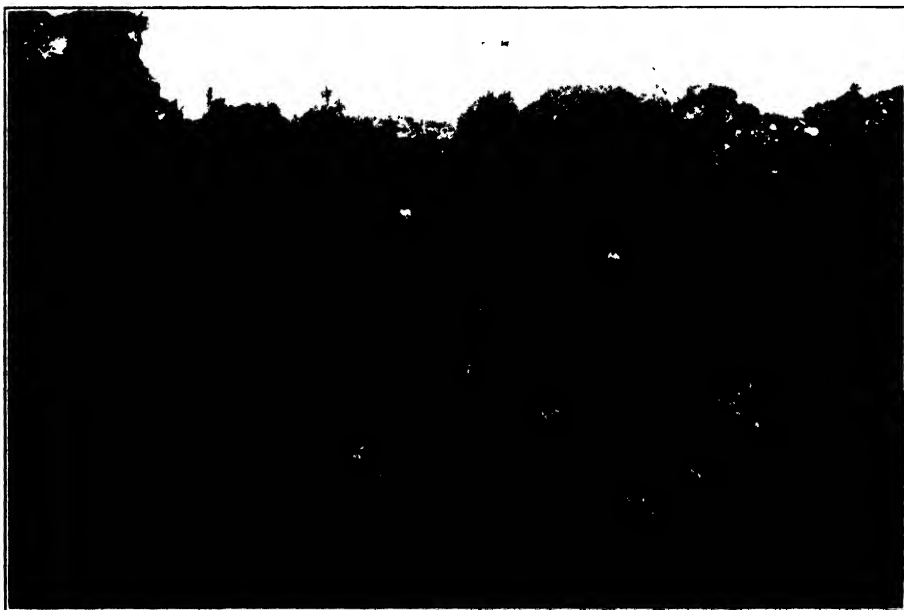


FIG. 5. Northern portion of *Andropogonetum scoparii* separated from the main grassland by a young forest salient to the right. In the *Myrica* clump to the right the little boy is sitting on a young *Acer rubrum* so as to give an unobstructed view of the oak forest in the background.

and Braun ('28) have each described natural grasslands with an abundance of *Juniperus virginiana*.

The red cedar demands light, and is intolerant of shade. In the grassland, the Junipers are strong and vigorous specimens (Figs. 3 and 4); near the forest edge they are visibly affected by the shade, and finally, about 150 to 300 feet within the forest, large dead cedars may be found. These latter trees most certainly started and grew in the open. Their age was estimated to be about 100 years. This would indicate that the forest has encroached into the grassland at the rate of 1 to 3 feet per year. The chart quadrat,

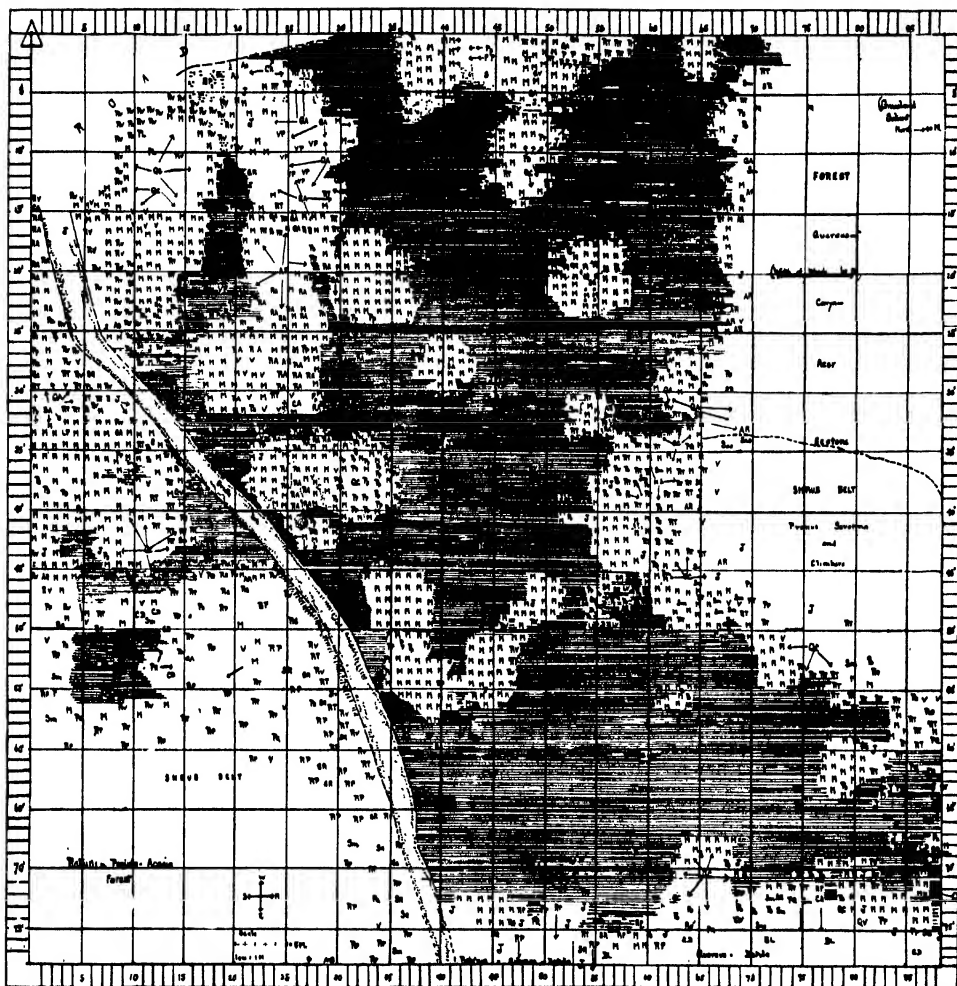


FIG. 6. Quadrat 78 by 88 meters, showing the relation of grassland to the *Myrica* association.

AR	<i>Acer rubrum</i>	QA	<i>Quercus alba</i>
AS	<i>Aster ericoides</i>	Qc	<i>Quercus coccinea</i>
BL	<i>Betula lenta</i>	Qp	<i>Quercus Prinus</i>
BP	<i>Betula populifolia</i>	Qvs	<i>Quercus velutina</i> —seedling
CA	<i>Carya alba</i>	RA	<i>Rubus allegheniensis</i>
CD	<i>Castanea dentata</i>	RC	<i>Rhus copallina</i>
D	<i>Chrysanthemum leucanthemum</i>	RP	<i>Robinia Pseudo-Acacia</i>
J	<i>Juniperus virginiana</i>	RT	<i>Rhus toxicodendron</i>
LV	<i>Linaria vulgaris</i>	RV	<i>Rubus villosus</i>
M	<i>Myrica carolinensis</i>	Sas	<i>Sassafras variifolium</i>
NS	<i>Nyssa sylvatica</i>	SA	<i>Solidago tenuifolia</i>
O	<i>Rumex acetosella</i>	Sm	<i>Smilax rotundifolia</i>
PL	<i>Polygonum convolvulus</i>	SR	<i>Solidago rugosa</i>
Po	<i>Quercus stellata</i>	V	<i>Vitis lubrusca</i>
Pp	<i>Prunus pennsylvanica</i>	Vp	<i>Vaccinium pennsylvanicum</i>
Pq	<i>Psedera quinquefolia</i>		Dead grass
Ps	<i>Prunus serotina</i>		Grassland

(Fig. 6), shows the number, position, and distribution of *Juniperus virginiana* in the grassland. The survey map (Fig. 9) presents the position of the grassland, shrub-area, and the forest region. The contour lines give the general topography.

Syngenetics or Vegetational Succession in the Grassland of High Hill

For the past 35 to 50 years, the biotic (human) factors disturbing the vegetation, especially the grassland on High Hill, have mostly or entirely ceased to operate. This gives the habitat and vegetation an opportunity of adjustment—to give expression to ecological and sociological constructiveness, by the production of vegetational changes, culminating finally in an edaphic as well as a climatic climax.

In the first place, the physiognomy of the vegetation on High Hill is changing. The prevailing or dominant vegetation (grassland) is being altered. This means the substitution of one dynamic-genetic unit by another of sociological importance.

According to Braun-Blanquet ('28, p. 275) "Succession of vegetation consists in the last analysis of the exchange (appearance and disappearance) of species, or of changes in the quantitative relations of species continuously present. Not every exchange of species is to be regarded as a stage of succession. Only when the existing equilibrium is obviously disturbed—the uniformity of the prevailing vegetation is visibly altered—are we justified in speaking of a substitution of one dynamic-genetic unit by another."⁴

STAGE I. (THE *Myrica carolinensis* ASSOCIATION WITH TWO PHASES)

The first single clearly marked step in the invasion of the *Andropogonetum scoparii* on High Hill may be designated as Stage I which was brought about by the *Myrica* association. This association invades the grassland, and, by the active constructive and destructive causative values of its species, transforms the ecological structure of the grassland association to that of a woody shrub association.

The Myrica Phase

The first phase of this transformation is caused by *Myrica carolinensis* which, as a pioneer migrant species of the association, invades the grassland and sends out roots in various directions a few inches below the surface of the gravelly soil. These roots produce vegetative shoots in their immediate vicinity and establishment is complete. The shoots soon grow into "bush"—

⁴ The book, "Pflanzensoziologie" by Braun-Blanquet, is sound, thorough, and informative—based primarily on the consideration of the dynamics of the species. An English translation is now being prepared by Drs. Conard and Fuller and will soon be published.

producing clumps of *Myrica*. Figures 3 and 4 show these clumps in the center and peripheral regions of the grassland association. Each clump functions as a dynamic center of further encroachment. The position and contents of these *Myrica* clumps are shown in the 78 by 88 meter chart quadrat (Fig. 6).

On High Hill a sharp line of tension or ecotone exists between the *Andropogonetum scoparii* and the woody shrubs of *Myrica*. The encroachment into the grassland is not only from dynamic centers but also by centripetal development from the peripheral regions of the grassland as well.

Bayberry clumps occur in various stages of development, from a single sprig to large clumps measuring several meters across. In the larger clumps secondary invaders have already made their appearance (see 78 by 88 meter chart quadrat, Fig. 6). In this connection, it is interesting to note Taylor's ('23, p. 22) report of *Myrica carolinensis* occurring in the Downs at Montauk which he considers a natural grassland. He says, "There are today hundreds of tiny patches of 'bush' scattered over the Downs almost without exception, the major portion of these islands is made up of Bayberry (*Myrica carolinensis*), very often associated with which will be *Rosa carolina* and perhaps the whole mass bound together with *Rubus procumbens* . . . or *Smilax glauca*." Taylor did not recognize the dynamic-genetic importance of *Myrica carolinensis*, nor did he follow the sequence of the stages in succession, but suggests it in his statement, "From this stage in the development of a patch which may start with a single sprig of Bayberry, and end with a forlorn and stunted tree in the center of it, no one knows how long a time may have elapsed" (*l. c.*, p. 23).

A study of one of the "mature" clumps of *Myrica* reveals further the story of plant succession as it occurs on High Hill. For this study, a clump of *Myrica* was selected which is situated at the intersection of the lines 32 and 37' on the 78 by 88 meter chart quadrat (Fig. 6).

Such a study reveals the following facts: *Andropogon scoparius*, being intolerant of shade, dies out beneath the *Myrica*—the tussocks near the center of the shrub-cluster perish while those in the peripheral region are weakened. Simultaneously with this change within the center of the association, the physico-chemical condition of the soil is changing, due to the accumulation of humus. This is formed by means of soil organisms which cause the decay of the dead grass, and of the dense mats of twigs and leaves of *Myrica*. Under the protection of the *Myrica*, the humus is kept from washing or blowing away, and the evaporation is reduced—moisture content increases. The habitat now forms a favorable seed bed.

In résumé: *Myrica carolinensis* proved itself to be a migrant species and capable of establishing itself in the grassland. It showed its dynamic destructive value in changing the light conditions so as to kill the bunch grass. It

shows highly dynamic-genetic constructive potentialities in being instrumental in bringing about profound changes in the habitat so as to produce an environment favorable for other plants to follow, finally leading to the climax forest described below.

The Prunus Phase

In response to the favorable conditions brought about by *Myrica carolinensis*, the second or intermediate phase is initiated: viz., seedlings of *Prunus serotina* and *P. pennsylvanica* appear in the center of clumps of *Myrica*. The latter species multiplies by suckering. The two species become readily established, and, by means of rapid growth, soon tower over the *Myrica* and smother the portion of it in their immediate vicinity, while that 3 to 4 feet in height still grows luxuriantly in the peripheral region of the clump, the whole giving the appearance of having been planned by a landscape artist. Figure 7 conveys the appearance of the *Myrica* clump with the species of *Prunus*, 14 ft. in height, growing in the center. The 8 by 10 meter chart quadrat (Fig. 8) demonstrates the floristic composition of the clump.

The *Prunus* species at first are strong and vigorous plants and function



FIG. 7. Clump of *Myrica carolinensis* invaded by the *Prunus* phase. The *Myrica*, about 4 ft. in height, is growing luxuriantly in the peripheral region, while the *Prunus* trees, about 14 ft. in height, occupy the central portion; Juniper trees are behind the clump.

as a dynamic force in changing the physiognomy of the vegetation. But they are soon overtaken by maladies which weaken them considerably or actually destroy them. *Prunus serotina* is violently attacked by black-knot, *Plow-rightia*, which checks it noticeably as a competitive force, while *P. pennsylvanica* ultimately succumbs to the attack of another fungus.

Following in the wake of the *Prunus* phase is a train of secondary invaders, chief among which are the following: *Rubus villosus* (*procumbens*), *Smilax rotundifolia*, *Psedera quinquefolia*, *Vitis labrusca*, and *Rhus toxicodendron*.

Rubus villosus possesses little or no dynamic-genetic qualities other than that of an invader; it is very intolerant of shade. It roots in the humus soil in the shade of the peripheral region of the *Myrica* clump and sends its runners for a meter or two between the tussocks of the *Andropogon scoparius* in the grassland, so as to obtain sufficient light, and is of no further consequence in the successional stages.

The climbers (lianas) do not always fill an important place in the development of the sere since they may or may not be present. It is better to think of them as accidental species so far as vegetational change is concerned on High Hill.

They are by their very nature destructive forces, and, when present, are highly important dynamic-genetic species of a destructive type. They take front rank as an agency in changing the physiognomy of a community of plants (Fig. 10). They respond chiefly to the need for support or for better illumination by attaching themselves to taller growing plants. The chief disadvantage of this feature to the species is that it causes the climbers to be more or less dependent.

In the *Myrica* clumps, the climbers in their search for light make their way up through the *Myrica* and *Prunus* growth in the central region of the clump and climb over the *Myrica*, in some cases forming a miniature canopy, and thereby producing more and more shade, and conserving yet more moisture in the soil. The increased shade aids in the complete destruction of the *Myrica* in the center of the clump. However, the *Myrica* in the competitive struggle, fights for the lost ground by sending up shoots in the ground layer. These in turn will finally be destroyed for want of light (see chart quadrat, Fig. 8).

The further migration into the grassland by the *Myrica* as a causative agent of succession, is as follows: In response to the operative competitive forces within an invaded clump (together with its natural proclivities) the *Myrica* at the periphery of these clumps pushes its way by root sprouts more and more into the grassland. Thus the *Myrica* clumps occupy a greater area. This provides for the extension of the *Prunus* phase and subspecies.

QUERCUS STAGE, II (*Quercetum albae*)*Quercus* Phase I

In these "mature" *Myrica* clumps near the center where the leaf mold is present and the moisture conditions favorable, seedlings of an oak or maple may be found. In the *Myrica* bush studied in detail (chart quadrat, Fig. 8),

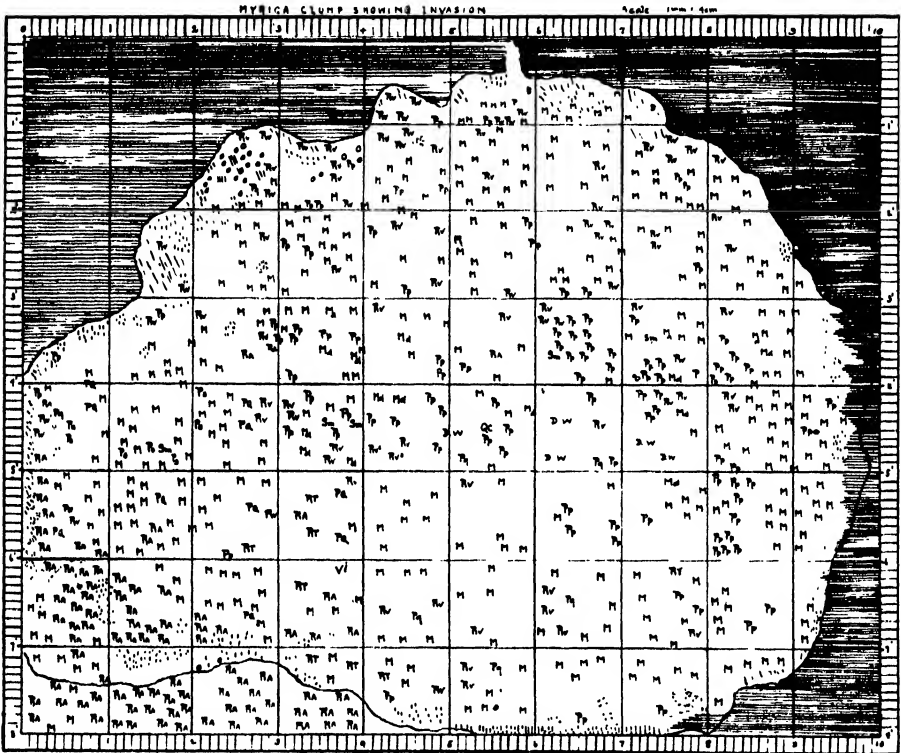


FIG. 8. Chart quadrat 10 by 8 meters, of the clump of *Myrica carolinensis* shown in figure 7.

⋮⋮⋮	Dead grass	Pq	<i>Psedera quinquefolia</i>
≡≡≡	Grassland	Qc	<i>Quercus coccinea</i>
DW	Dead wood	RA	<i>Rubus allegheniensis</i>
M	<i>Myrica carolinensis</i>	Rv	<i>Rubus villosus</i>
Md	Dead <i>Myrica</i>	RT	<i>Rhus toxicodendron</i>
O	<i>Rumex acetosella</i>	Sm	<i>Smilax rotundifolia</i>
Pp	<i>Prunus pennsylvanica</i>		

near the center is a young *Quercus coccinea*. It is about 5 feet tall (in 1928), and is in a fair way of establishing itself there. In the chart quadrat, its position is marked by the letters QC. Although crowded, it is healthy and gives every indication that it will soon outgrow its neighbors and will tower above them as the *Prunus* had towered above the *Myrica*. The oak trees, as

noted below, will cause, in turn, the destruction of, or at least the inhibition of the *Myrica* association by their shade, in combination with various edaphic factors.

What has been said of succession up to this point (save the Juniper invasion) has taken place in the aforementioned clump of *Myrica*. The same processes of development (or changes of vegetation) are proceeding in various stages in other *Myrica* clumps as well (see 78 by 88 meter chart quadrat, Fig. 6).

Shrub Region

The ever enlarging clumps of *Myrica carolinensis*, with their invaders, eventually come in contact with other similar clumps and "fuse" in the sense that each loses its identity. Further expansion of the *Prunus* species and climbers will destroy the *Myrica* between. By this means a shrub region with the *Prunus* and lianas as characteristic species is formed. An examination of the 78 by 88 meter quadrat (Fig. 6) will show that the *Myrica* completely surrounds the *Andropogonetum scoparii*, and that just behind the *Myrica* is a shrub belt which was initiated and is being enlarged through the dynamic-genetic values of the species of the *Myrica* association. The contour map (Fig. 9) shows that a shrub belt of varying width intervenes between the

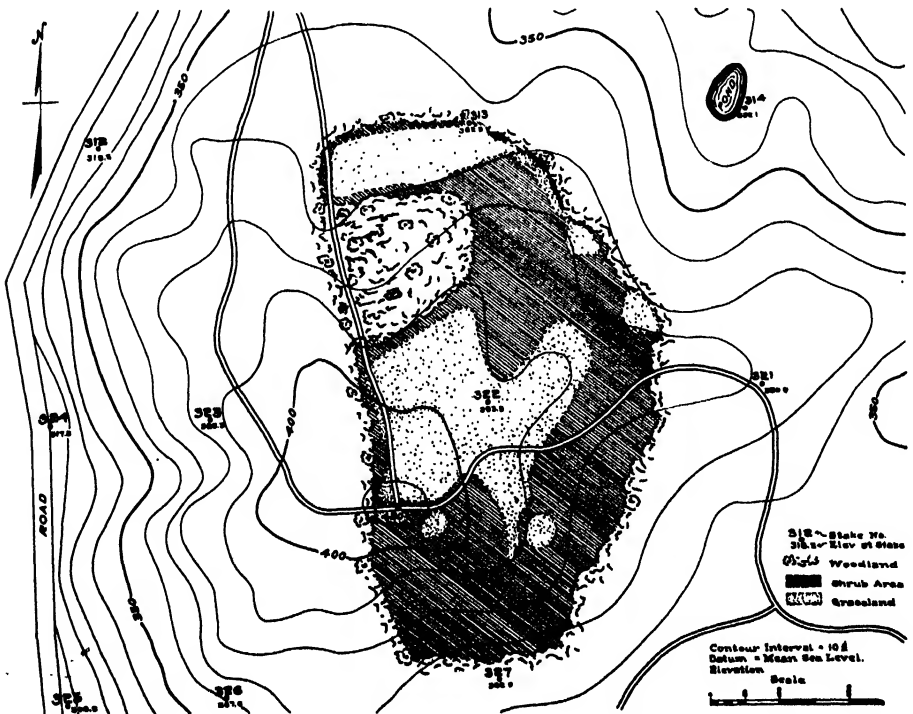


FIG. 9. Grassland, shrub, and forest regions. Topographical survey of High Hill with contour lines showing elevations.

grassland and the forest. There is no doubt that the vegetation in the shrub area has been interfered with in recent years, or else the forest would have kept more closely on the "heels" of the advancing *Myrica*. In fact, Mr. Robert De Forest, the owner of this land, told the writer that he had nurtured certain trees, *Quercus coccinea*, *Q. alba*, and *Acer rubrum*, in the south-west corner, for the last 35 years. These trees are now about 30 or more feet in height and sturdy (Fig. 6).

The shrub belt is of interest, too, because of the presence of other species of plants, the distribution of which and the successions from grassland through

TABLE II. *Belt transect 4 meters wide*

Numbers at the head of the columns represent quadrats along the transect. Numbers in the body of the table are cover values indicating abundance on the scale of 1 to 5.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
<i>Andropogon scoparius</i>	5	5	5														
<i>Polytrichum piliferum</i>	3	3	3														
<i>Cladonia rangiferina</i>	3	3	3														
<i>Cladonia symphyarpa</i>	3	3	3														
<i>Hypericum gentianoides</i>	2	2	2														
<i>Hieracium scabrum</i>	+	+	+														
<i>Rumex acetosella</i>	+	+															
<i>Myrica carolinensis</i>			+	5	+	+	1	+	+	+		+					
<i>Prunus serotina</i>				+	+	+						+					
<i>Prunus pennsylvanica</i>				1	1	1						Dead					
<i>Solidago rugosa</i>				1	1	2	+					Dead					
<i>Rhus toxicodendron</i>				2	3	5	4	5	3	1	1	2	2	2	2	+	+
<i>Psedera quinquefolia</i>				+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Rhus copallina</i>				+	+	+						+	+	+	+	+	+
<i>Vitis labrusca</i>				+	+	+	+	+				+	+			+	+
<i>Rubus allegheniensis</i>				+	+	+	+	+									
<i>Aster ericoides</i>				+	+												
<i>Smilax rotundifolia</i>				+	+	2	1	+	1	1	1	+	+	+	+	+	
<i>Rubus villosus</i>				1	1	4	+	+	2	2	2	1	1	+	1		
<i>Acer rubrum</i>				+		+	+	+	5	4	1	2	2	2	2		
<i>Juniperus virginiana</i>						1		+	+		Sickly	+	+	+	+	Sickly	
<i>Quercus alba</i>						1	1	+	2	1	2	5	5	5	5	2	2
<i>Betula lenta</i>						1	+	1				+	+	+	+	5	5
<i>Castanea dentata</i>						1	1	1	+			+	+	+	+		
<i>Solidago linearis</i>						3	2	1									
<i>Quercus marylandica</i>						+		+	+			1	1	1	1		
<i>Quercus velutina</i>									4	4	4	+	+	+		1	1
<i>Carya alba</i>						+			+	+	+	+	+	+			
<i>Polytrichum Ohioense</i>									+	+	+						
<i>Dicranella heteromalla</i>						+	1	+									
<i>Webera sesilis</i>							+										
<i>Polytrichum commune</i>								+	2	1	3	2	+	+	+	+	+
<i>Catherinea angustata</i>								+	+	1	1	+	+	+	+	+	+
<i>Gaylussacia baccata</i>								+	2	1	1	2	+	+	+		+
<i>Vaccinium pennsylvanicum</i>								+	1	+	+	1	+	+		+	+
<i>Lyssmachia quadrifolia</i>								+	+	+	+	+	+			+	+
<i>Smilacina racemosa</i>								+	+	+	+	+	+	+		+	+
<i>Chimaphila maculata</i>								+	+	+	+	+	+		+	+	+
<i>Cornus florida</i>								+	+	+	+	+	+	+	+	+	+
<i>Quercus Prinus</i>													+	+	+	+	+
<i>Betula populifolia</i>														+	+	+	+
<i>Nyssa sylvatica</i>														+			

shrub to forest are clearly shown by the series of quadrats along the 4 meter wide belt transect (Table II). The belt transect extends from the grassland through the ecotones in to the young forest salient, situated as shown on the chart quadrat (Fig. 6) on the north-west corner marked "Forest" (*Quercus-Carya-Acer*).

The belt transect clearly shows that the ecotone (Columns 3-4) between grassland (Columns 1-3) and shrubs (Columns 5-6) is sharply defined, while the shrubs and forest merge without any definite line of demarcation. The various steps in succession described above are well illustrated by the series of quadrats in the belt transect, but not so certainly marked as those studied in clumps of *Myrica* in various stages of development. Table II shows at a glance, by means of the cover values, that *Myrica*, *Prunus*, and the climbers are the characteristic species of the shrub belt. In the same way, the top layer of the forest is shown to be composed of species of *Quercus*, *Acer*, and *Carya*, with a characteristic ground layer.

Forest Region

QUERCUS PHASE II

The oak or maple trees become established, and the shade of their overhanging branches eventually drives out the *Myrica* association (see 78 by 88 meter chart quadrat, Fig. 6, south-west corner). Some shrubs as well as remnants of the grassland still remain. Beneath the oaks and maples another group of plants comes in which is more or less typical of the forest floor, namely:

<i>Vaccinium pennsylvanicum</i>	<i>Polygonum dumetorum</i>
<i>V. vacillans</i>	<i>Chimaphila maculata</i>
<i>Helianthemum canadense</i>	<i>Dicranum scoparium</i>
<i>Rubus hispidus</i>	<i>Polytrichum Ohioense</i>
<i>Rhus toxicodendron</i>	<i>P. commune</i>
<i>Rumex acetosella</i>	<i>Amanita phalloides</i>

The next and final stage in the sere initiated by *Myrica carolinensis* is the mixed oak climax forest. While the forests on the sides of High Hill are not at all homogenous as to species, the list for the western slope composed of three layers (Table III) is more or less typical.

TABLE III. List of plants on the western slope of High Hill, Long Island, arranged according to layers

TOP LAYER

From twenty feet or more in height

<i>Quercus velutina</i>	<i>Q. alba</i>
<i>Q. Prinus</i>	<i>Carya glabra</i>

MIDDLE LAYER

Fifteen feet to ground layer

<i>Cornus florida</i>	<i>Solidago bicolor</i>
<i>Castanea dentata</i>	<i>Kalmia latifolia</i>
<i>Gaylussacia baccata</i>	<i>Lyonia mariana</i>
<i>Juniperus virginiana</i> (dying)	<i>Deschampsia flexuosa</i>
<i>Luzula campestris</i>	<i>Dentonia spicata</i>
Seedlings of oak	

GROUND LAYER

One foot or less in height

<i>Vaccinium pennsylvanicum</i>	<i>Epigaea repens</i>
<i>V. vacillans</i>	<i>Dicranella heteromella</i>
<i>Smilax glauca</i>	<i>Pohlia nutans</i>
<i>Polytrichum Ohioense</i>	

Under the protection of the invading forest the sparsely scattered seedlings of oak and black locust that appear in the *Andropogonetum scoparii* apparently will be able to establish themselves. This agrees with Taylor's ('23, p. 49) observation as regards the Downs. He states "The oaks reach really exposed places toward the tops of the Downs only rarely, and with apparently great difficulty . . . become established; once the start is made, it seems only a matter of time, due to increasing protection from the wind as the growth becomes gradually thicker . . . infinitely slow as time goes, but from all the evidence available, as certain as the tides."

If the oak seedling would succeed on High Hill the development of the sere would be immensely shortened, as indicated on the left side of diagram of secondary succession (Fig. 10).

Robinia-Pseudo-Acacia depends chiefly on number of individuals to overcome the competitive forces of the grassland and shrubs. On the southeast portion of High Hill at the edge of the grassland is a single locust seedling; in the nearby shrubs there are several young locusts. As one penetrates the shrub-belt to the southeast, the locust trees become more numerous and taller, until, a few hundred feet farther, an almost pure stand of locust may be found. In this *Robinietum-Pseudo-Acaciae*, the trees are 80 or more feet in height and festooned to the very top with the climbers, *Rhus toxicodendron*, *Vitis labrusca*, *Psedera quinquefolia*, and *Smilax rotundifolia*. Figure 11 shows just the upper edge of this jungle-like assemblage of plants. One by one, the locust trees with their loads of vines fall to the ground, or else, unable to crash through the tangled mass of vegetation, rest at various angles in the air, propped up by the other trees. The lianas which climb upon the trees or hang in great festoons, because of their numerous leaves, contribute to the formation of a dense forest canopy. In the lower layer, growing in the comparatively dense shade, sparsely scattered, are shrubs from 3 to 15 feet in height: *Sassafras variifolium*, *Cornus florida*, *Benzoin aestivale*, *Betula lenta*, *Lonicera japonica*. On the ground are fallen locust trees covered with *Rhus*

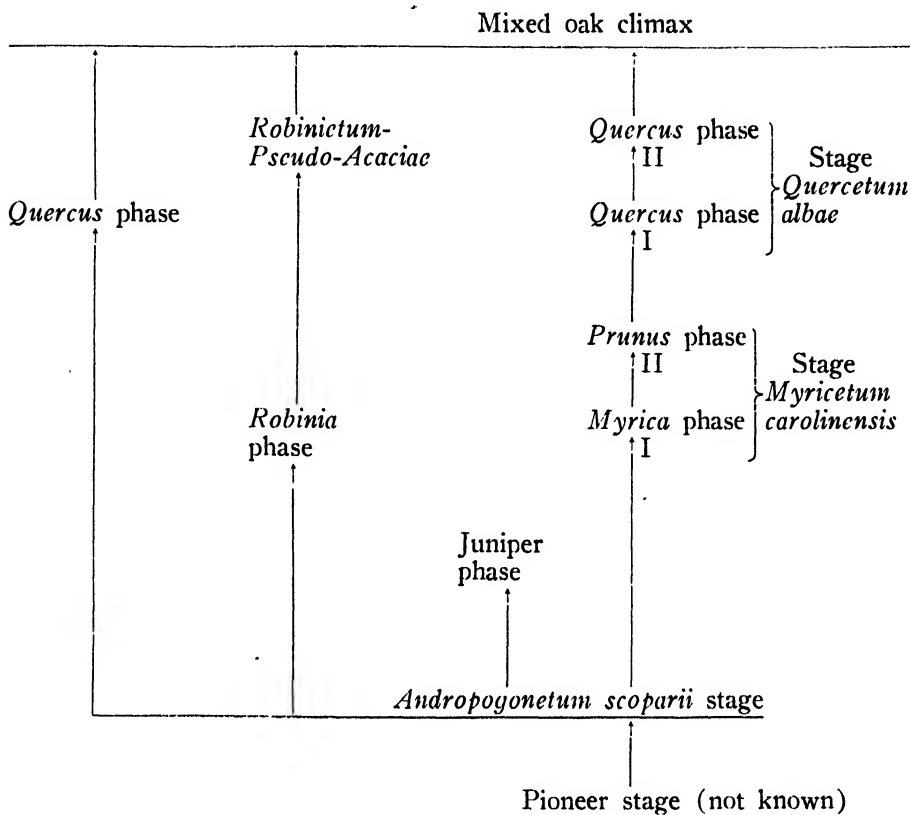


FIG. 10. Diagram of the secondary succession on High Hill.

toxicodendron, or with some of the other climbers mentioned above; also, *Smilacina racemosa*, *Arisacma triphyllum*, *Impatiens biflora*, *Catherinea augustata*, *Mnium hornum*, *Mnium cuspidatum*.

When the festooned trees fall, they are succeeded at the lower edge of the slope by the *Quercus-Carya* association.

The following interesting group of "road-side" plants occurs along the bridle path (Fig. 6):

Agrostis alba
Anthoxanthum odoratum
Cladonia cristatella
Hieracium Gronovii
Juncus tenuis

Panicum meridionale
Plantago rugelii
Poa triflora
Trifolium repens
Phleum pratense

Table IV gives a partial list of the plants on High Hill, arranged in alphabetical order.

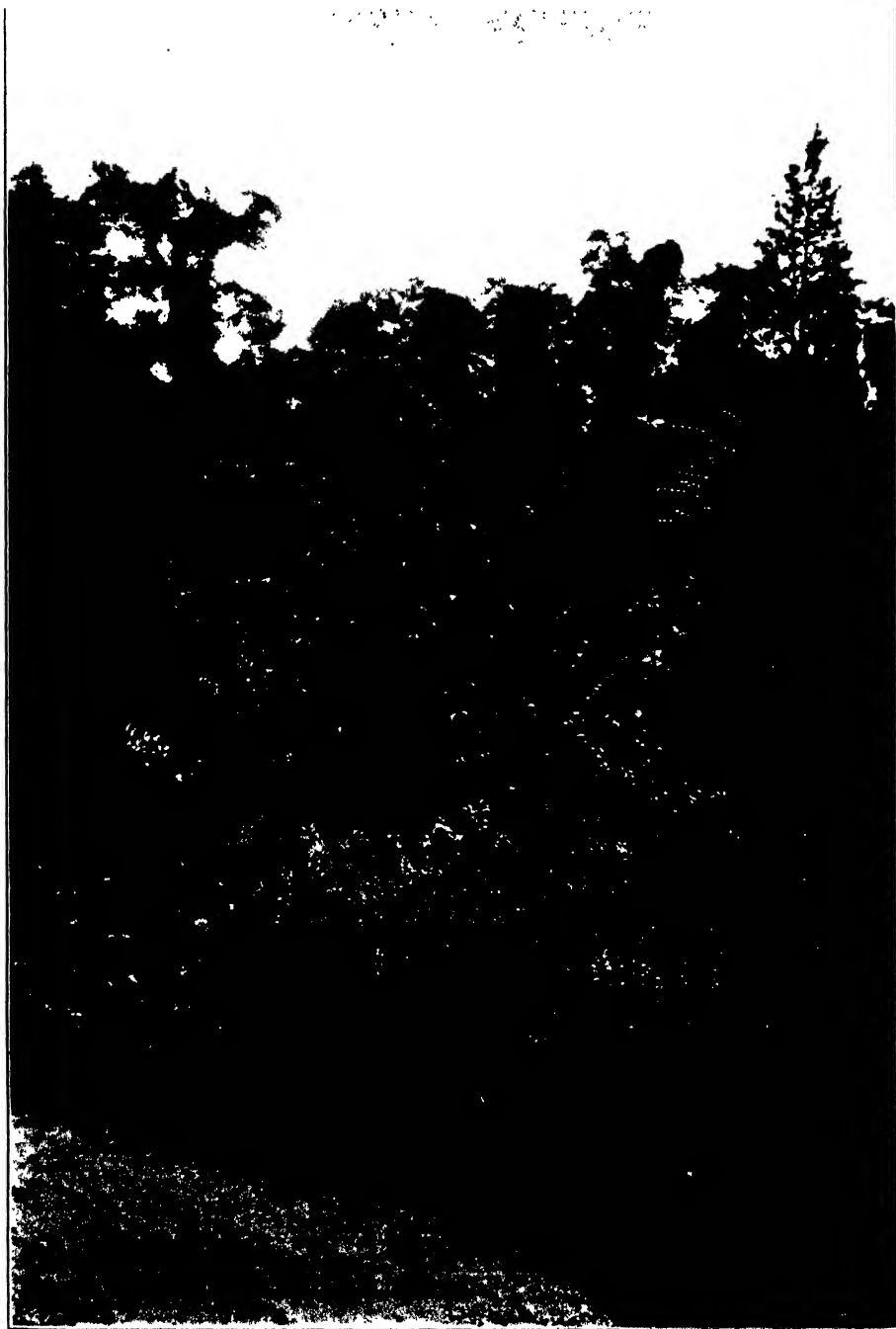


FIG. 11. In the background are locust trees festooned with the lianas. In the foreground is the shrub region, with a colony of *Solidago rugosa*.

TABLE IV. *Partial list of plants growing on High Hill, Long Island, New York*

- | | |
|--|---------------------------------------|
| 1. <i>Acer rubrum</i> | 51. <i>Gaylussacia baccata</i> |
| 2. <i>Agrimonia gryposepala</i> | 52. <i>Gnaphalium polycephalum</i> |
| 3. <i>Agrostis alba</i> | 53. <i>Helianthemum canadense</i> |
| 4. <i>Amanita phalloides</i> | 54. <i>Hieracium Gronovii</i> |
| 5. <i>Andropogon scoparius</i> | 55. <i>Hieracium scabrum</i> |
| 6. <i>Antennaria plantaginifolia</i> | 56. <i>Hypericum gentianoides</i> |
| 7. <i>Anthoxanthum odoratum</i> | 57. <i>Hypericum perforatum</i> |
| 8. <i>Aspidium marginale</i> | 58. <i>Ilex verticillata</i> |
| 9. <i>Aspidium spinulosum</i> | 59. <i>Impatiens biflora</i> |
| 10. <i>Asplenium Filix-femina</i> | 60. <i>Juncus tenuis</i> |
| 11. <i>Aster divaricatus</i> | 61. <i>Kalmia latifolia</i> |
| 12. <i>Aster ericoides</i> | 62. <i>Lactuca canadensis</i> |
| 13. <i>Aster lateriflorus</i> | 63. <i>Leucobryum glaucum</i> |
| 14. <i>Arisaema triphyllum</i> | 64. <i>Linaria canadensis</i> |
| 15. <i>Berberis thunbergii</i> | 65. <i>Linaria vulgaris</i> |
| 16. <i>Benzoin aestivale</i> | 66. <i>Lonicera japonica</i> |
| 17. <i>Betula lenta</i> | 67. <i>Luzula campestris</i> |
| 18. <i>Betula lutea</i> | 68. <i>Lycopodium dendroideum</i> |
| 19. <i>Betula populifolia</i> | 69. <i>Lycopodium lucidulum</i> |
| 20. <i>Botrychium obliquum</i> | 70. <i>Lyonia mariana</i> |
| 21. <i>Botrychium obliquum</i> , var. <i>dissectum</i> | 71. <i>Lysimachia quadrifolia</i> |
| 22. <i>Bryum caespiticium</i> | 72. <i>Medeola Virginiana</i> |
| 23. <i>Carex pennsylvanica</i> | 73. <i>Maianthemum canadense</i> |
| 24. <i>Carya glabra</i> | 74. <i>Mitchella repens</i> |
| 25. <i>Castanea dentata</i> | 75. <i>Mnium cuspidatum</i> |
| 26. <i>Catherinea angustata</i> | 76. <i>Mnium hornum</i> |
| 27. <i>Catherinea undulata</i> | 77. <i>Monotropa uniflora</i> |
| 28. <i>Ceratodon purpureus</i> | 78. <i>Mycena galericulata</i> |
| 29. <i>Chimaphila maculata</i> | 79. <i>Myrica carolinensis</i> |
| 30. <i>Chrysanthemum leucanthemum</i> | 80. <i>Myrica asplenifolia</i> |
| 31. <i>Chrysopsis mariana</i> | 81. <i>Nyssa sylvatica</i> |
| 32. <i>Cladonia cristatella</i> | 82. <i>Panicum meridionale</i> |
| 33. <i>Cladonia rangiferina</i> | 83. <i>Phleum pratense</i> |
| 34. <i>Cladonia symphycarpa epiphylla</i> | 84. <i>Pohlia nutans</i> |
| 35. <i>Cornus florida</i> | 85. <i>Phytolacca decandra</i> |
| 36. <i>Cyperus filiculmis</i> | 86. <i>Pinus rigida</i> |
| 37. <i>Cyripedium acaule</i> | 87. <i>Pinus strobus</i> |
| 38. <i>Danthonia spicata</i> | 88. <i>Plantago Rugellii</i> |
| 39. <i>Deschampsia flexuosa</i> | 89. <i>Platanus occidentalis</i> |
| 40. <i>Dicranum scoparium</i> | 90. <i>Poa triflora</i> |
| 41. <i>Dicranella heteromalla</i> , var. <i>orthocarpa</i> | 91. <i>Polygonum dumetorum</i> |
| 42. <i>Epigaea repens</i> | 92. <i>Polystichum acrostichoides</i> |
| 43. <i>Epipactis pubescens</i> | 93. <i>Polytrichum commune</i> |
| 44. <i>Erigeron annuus</i> | 94. <i>Polytrichum Ohioense</i> |
| 45. <i>Eupatorium hyssopifolium</i> | 95. <i>Polytrichum piliferum</i> |
| 46. <i>Eupatorium purpureum</i> | 96. <i>Populus grandidentata</i> |
| 47. <i>Fagus grandifolia</i> | 97. <i>Prunus avium</i> |
| 48. <i>Festuca octoflora</i> | 98. <i>Prunus maritima</i> |
| 49. <i>Fraxinus americana</i> | 99. <i>Prunus pennsylvanica</i> |
| 50. <i>Funaria hygrometrica</i> | 100. <i>Prunus serotina</i> |
| | 101. <i>Psedera quinquefolia</i> |

- 102. *Pyrus arbutifolia*
- 103. *Quercus alba*
- 104. *Quercus coccinea*
- 105. *Quercus marilandica*
- 106. *Quercus Prinus*
- 107. *Quercus velutina*
- 108. *Rhus copallina*
- 109. *Rhus glabra*
- 110. *Rhus toxicodendron*
- 111. *Robinia Pseudo-Acacia*
- 112. *Rubus allegheniensis*
- 113. *Rubus hispidus*
- 114. *Rubus villosus*
- 115. *Rumex acetosella*
- 116. *Sambucus canadensis*
- 117. *Sanicula canadensis*
- 118. *Sanicula marilandica*
- 119. *Sassafras variifolium*

- 120. *Sericocarpus asteroides*
- 121. *Smilacina racemosa*
- 122. *Smilax glauca*
- 123. *Smilax rotundifolia*
- 124. *Solidago bicolor*
- 125. *Solidago juncea*
- 126. *Solidago tenuifolia*
- 127. *Solidago nemoralis*
- 128. *Solidago rugosa*
- 129. *Stenophyllus capillaris*
- 130. *Symphoricarpos vulgaris*
- 131. *Trifolium repens*
- 132. *Vaccinium pennsylvanicum*
- 133. *Vaccinium vacillans*
- 134. *Verbascum Thapsus*
- 135. *Viburnum acerifolium*
- 136. *Vitis labrusca*
- 137. *Webera sessilis*

Summary

1. The grassland which covers a portion of High Hill, Long Island, represents a stage—*Andropogonetum scoparii*—in a secondary succession.

2. The *Andropogon scoparius* association has existed on High Hill for a century and a half—probably much longer.

3. The grassland was able to hold out against invasion by other plants primarily because of the equilibrium established by the socializing plant forms: *Andropogon scoparius*, two lichens, and one moss. The former functions as a consolidating force in the association; the two latter contribute mineral nutrient and formation of soil.

4. *Myrica carolinensis* possesses highly dynamic-genetic potentialities of sociological importance; destructive as well as constructive to the plant community.

a. It is capable of invading the *Andropogonetum scoparii* and becoming established.

b. It changes the habitat so that a trail of secondary invaders comes in; these become established and through competition and succession make it possible for

c. Trees of the surrounding forest to come in, and in turn, become established.

d. Thus through the mediation of *Myrica carolinensis* the forest is able to invade the grassland.

5. Because of the demonstrated qualities of the sociological constructiveness of *Myrica carolinensis* it is recommended as a means of bringing denuded, abandoned, or other land to forest in the eastern and northeastern United States.

6. The vegetation of High Hill is separated into well defined belts, viz., grassland, shrubs, and forest.
7. The ecotones and successions have been established by means of permanent quadrats located in relation to a United States Geodetic and Coastal Survey Triangulation Station. Thus they will always be accessible.
8. A partial list of the plant species on High Hill is given.

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REVIEWS

PLANT ECOLOGY¹

As stated in the preface, this volume is the outgrowth of many years of research and teaching by both authors. Other reviews of the book have appeared,² but the year which has elapsed since its publication has afforded the opportunity of very detailed study of its content. A few of the comments which follow were suggested by some part of the text, but are somewhat extraneous; they are enclosed in brackets.

In Chapter 1, on origin, development, and structure of vegetation (p. 6), the authors speak of "vegetation" as a single abstract entity. Their analogies between communities of varying rank (these being the parts of this entity) and the parts of an individual plant do not seem to be helpful. Otherwise the discussion is clear. The account of methods of studying vegetation in Chapter 2 includes convincing demonstrations from recent work, notably that of range ecologists, of the value and adaptability of various quadrat methods, as affording bases of comparison of herbaceous cover before and after experimental treatment, or to study changes over considerable periods, or to compare the same vegetation-type in localities differing in rainfall or other environmental variable. Effects of repeated clipping upon grass quadrats, are described. [No one seems to have tried clipping experiments on vegetation made up of dicot herbs; the result might be quite different. Another point with respect to clipping experiments is that they are very different from actual grazing, in which mechanical effects of trampling are so often of major influence.] Transects, bisects, growth-ring and burn-scar studies, many types of experimentation, and methods of mapping vegetation, are described and exemplified.

The third chapter, The Units of Vegetation, and the next, Plant Succession, form a condensed yet adequate picture of the views of the authors. Some ecologists believe this picture to be somewhat too orderly and too simple to fit the facts of vegetation as they are found. Chapters 5 to 8 deal with the details of succession, beginning with its causes: *initial*, continuing or *ecesis*, and stabilizing or *climatic*. Chapter 7, Competition and Invasion, is of special value in its presentation of recent studies of competition, largely those of the authors themselves, with H. C. Hanson (Carnegie Publ. no. 398, 1929). This subject is becoming increasingly important in crop ecology.

¹ Weaver, John E., and Clements, Frederic E. *Plant ecology*. xx + 520 pp. New York, McGraw-Hill Book Co. 1929. \$5.00.

² Ramaley, *Science*, 70: 218-219, Aug., 1929; Bates, *Jour. of Forestry*, 27: 856-858, 1929; Fuller, *Botanical Gazette*, 88: 452-454, 1929; Huber, *Zeitschr. f. Bot.*, 22: 335-336, 1929; Brierly, *Ann. Applied Biol.*, 17: 398-399, 1930.

We are still at a loss, however, in experiments involving critical knowledge of available soil-moisture values and of distribution of moisture in the soil. The authors' control of soil moisture does not seem to be satisfactory. The hygroscopic coefficient is not a trustworthy zero-point from which to estimate available water-content. The authors do not cite the recent soil-moisture studies by F. J. Veihmeyer and A. H. Hendrickson,³ showing among other things that the zero-point for available moisture must be determined directly for each soil. The appearance in English (since "Plant Ecology" was published) of Maximov's book⁴ will further contribute toward a better understanding of soil moisture and plant growth. Weaver's experiment with sunflowers on competition for water (p. 137 of the text) is not really that; it does give a valuable expression of the severity of competition for underground space, since crowding of plants necessarily decreases the volume of soil available to each root system. The underground parts of plants as they actually grow do not compete for water alone, and it is probable that experiments can not yet be devised which will measure such competition. Chapter 8, Reaction and Stabilization, describes the modification by vegetation of the physical environment.

Chapters 9 to 13 treat of the factors of the habitat. These are placed in three groups: direct, indirect, remote. Perhaps it is not intended that the lists of factors be complete, and it seems that only terrestrial habitats are considered. It is a little surprising to find that temperature is given only as an indirect factor. [The classification of environmental influences is a vexing problem, and probably no single published treatment is satisfactory. An article by Townsend⁵ may here be commended for its excellent distinction of influences as of three kinds: media, factors, and controls. Although some of the detailed examples given by Townsend may not be helpful, the article should be mentioned in every text on ecology.] After the introduction to the subject of factors, Chapter 9 describes in detail those of the soil, giving an excellent résumé of modern views of the soil as a developed entity with a character and life-history which is dependent upon climate and vegetation as well as upon the parent material. [A paper too recent to be cited in the text, by Shaw,⁶ should be consulted in this connection, and others of his writings, especially those dealing with soil-moisture⁷ and with classification of soils, will be of great value to ecologists.] The remainder of Chapter 9 describes

³ Veihmeyer, F. J., and Hendrickson, A. H. *Plant Physiology*, 2: 71-82, 1927; 3: 355-357, 1928; *Proc. & Papers 1st Internat. Congr. Soil Sci., Washington, D. C.*, 3: 498-513, 1928; *Proc. Am. Soc. Hort. Sci.*, 63: 105-108, 1929.

⁴ Maximov, N. A. The plant in relation to water. Translated by R. H. Yapp. London, George Allen and Unwin, Ltd. 1929.

⁵ Townsend, C. H. T. An analysis of insect environments and response. *Ecology*, 5: 14-25, 1924.

⁶ Shaw, C. F. Potent factors in soil formation. *Ecology*, 11: 239-245, 1930.

⁷ Shaw, C. F. The normal moisture capacity of soils. *Soil Science*, 23: 303-317, 1927.

the manner of working of the various soil factors, and gives methods for determining their values. Chapter 10, Relation of Underground Plant Parts to Environment, contains a wealth of material, chiefly from Dr. Weaver's own work, and includes many figures showing extent and distribution of root systems and their responses to peculiarities of soil.

Humidity, wind, and evaporation are the subjects of Chapter 11, with illustrations of their influences and of standard methods of determining their magnitudes. [Two recently-developed instruments may be mentioned in addition: McAdie's multi-scale wet-bulb thermometer, with which humidity values both relative and absolute are obtained without resorting to tables; and the 3-cup anemometer, which has smaller errors than the 4-cup type.]⁸ Temperature and light are discussed in the next two chapters. Chapter 14, Plant Response as a Measure of Environment, consists of descriptions of several types of phytometers and their working.

Chapter 15, Adaptation to Water, deals successively with hydrophytes, mesophytes, and xerophytes, with 27 pages devoted largely to water-conserving devices of the third group. It is very interesting to contrast this account with Maximov's new book, in which the very rapid use of water under xeric conditions, by xerophytes as well as mesophytes, is so greatly emphasized. There is a seeming paradox in this contrast which calls for much further investigation into water-relations. One recalls that the plants, cultivated as well as native, which we find tolerating dry-land environments, are almost without exception xerophytes.

Relations between plants and animals are discussed in Chapter 16. The common words for these relations, *interaction* and *interrelations*, are not used. The relations "are termed *coactions* and together with the action of the habitat upon organisms and the reaction of the plants upon the habitat make up the three major processes of every community" (p. 378). Reactions of animals upon the habitat are not mentioned. It is more than implied that dependence of animals upon physical environment is almost negligible as compared with dependence upon the plants. Certain animal ecologists, notably Shelford, incline to a nearly opposite opinion. It seems apparent that neither physical nor plant factors can be neglected, and that the proportion of influence attributable to the two groups of factors must vary with the animal and with conditions. Eleven pages are devoted to relations in pollination; very condensed accounts of the rôle of animals in dispersal of plant parts, effects of grazing animals and rodents, with brief mention of the influence of man upon vegetation and in introducing plants or animals into new areas, conclude this part of the book.

The next chapter is entitled Plants and Plant Communities as Indicators.

⁸ There is also newly available a hygrothermograph which gives the record for humidity below that for temperature, on a separately ruled part of the sheet. Distortion, due to movement of the pens in an arc, is in one direction only, and there is no confusion of rulings as in the old type of record sheet.

It is a noteworthy selection. Indicators of agriculture, of soil types, of alkali, of grazing potentialities, overgrazing, forest climate, former existence or possible establishment of forest, are given, and the usefulness of natural plant cover in the classification of land is described. The last chapter, 18, is 57 pages long, and though it gives an immense amount of the most essential information on the climax formations of North America, is necessarily rather condensed. The first few pages deal with the nature of climaxes, tests of a climax, and the concepts of preclimax and postclimax. A classified list of formations (climaxes) and their constituent associations then follows. For the sake of students, the list might well be expanded sufficiently to give specific names of the principal dominants which lend their names to communities, and in a few cases some indication of geographic position. The climaxes are then described in order. The dominants of each association, the relations of each association to the climate, to the climax of which it is a part, and to associations of neighboring climaxes, are adequately discussed. Many ecologists will not agree with certain details of treatment. Some will not agree with the separate recognition of a lake state forests climax dominated by *Pinus strobus* and *Tsuga*. Some may not agree with the omission as separate climaxes of the vegetation of the southeastern coastal plain and of the desert scrub of the New Mexico-Chihuahua area east of the Sierra Madre. But Dr. Clements gives strong reasons for their omission. He has consistently applied his criteria of classification, in which the application of subclimax and postclimax concepts plays a leading rôle.

In the opinion of the reviewer, this rôle is somewhat over-emphasized, and there seems to be a tendency to view this very complex subject (the classification and explanation of the vegetation of a continent) as one that is fundamentally quite simple once one is familiar with the facts. A suggestion of this view may be glimpsed from this quotation from near the beginning of the chapter (p. 424): "As a consequence, each formation or association plays a double rôle. It is a preclimax to its more mesophytic neighbor, and a post-climax to its more xerophytic one, though under the fairly static conditions of a major climatic phase the movement is only a potential one." This rather suggests a simple linear arrangement of climaxes, all in one gradient or series differing only in quantity of water available. There must be many more respects than this principal one in which climates and soil conditions vary one from another. Qualitatively differing combinations of soil, rainfall, temperature, and seasonal peculiarities, must result in rather complicated combinations of response on the part of the hundreds of dominant species of plants, each, as some ecologist has said, a law unto itself. Many of these dominants can and do assume different rôles with different conditions. Furthermore the environmental complexes have a regional unity in which the historic element must play a large part. Some readers will not agree that the assemblage of xeric southeastern pines should be relegated to a subclimax rôle merely because they are much more abundant because of fire. The implication that all

of them would disappear if fire were entirely prevented requires proof. Peculiarities of soil or of history may well account for part of the abundance of pines in the sandy lands of the coastal plain. Furthermore, if fire is a constantly recurring condition in a certain climate, then it is a feature of that climate, and as expectable as rainfall, though far more irregular.

With regard to the much greater prevalence of desert scrub in the Chihuahua-New Mexico-West Texas area than formerly, we owe much to Dr. Clements for emphasizing the fact that overgrazing has resulted in the spread of creosote bush at the expense of grassland, and that protection from grazing is followed by increase of grassland. Yet it is important for ecologists to recognize that the grasslands with least rainfall are most subject to the hazard of overgrazing, and therefore most liable to invasion by and permanent intermixture or alternation with desert scrub associations. The hazard of overgrazing is a corollary to climate in desert or in dry-grassland regions with minimum rainfall, as seen also in the valleys of California and in the "dry belt" of the short-grass plains of Colorado (average rainfall 7 to 13 inches; lowest minimum 3.78). Presumably the hazard of overgrazing by native animals during dry years antedated white settlement in North America, just as it is common today in even the less populated parts of Central Africa. If so there has probably been for many thousands of years climax desert scrub, with desert grassland also, in Chihuahua, west Texas, and southern New Mexico. There has probably been a limited area of desert scrub in the south end of the San Joaquin valley, and one or a few limited areas of climax short-grass in the dry plains 20 to 80 miles east of the Colorado Front Range. The short-grass and desert scrub are of course more prevalent now than formerly, but it may be doubted that they were recently non-existent in the areas mentioned.

One other application of the subclimax concept requires discussion. The eastern part of the prairie which alternates with forest in eastern Iowa, Illinois, and northern Indiana, is treated in "Plant Ecology" as the *subclimax prairie* because it occupies an area regarded as having a forest climate, and because of demonstrated tendency for forest to replace prairie. This tendency is slow; it has manifested itself only in certain places and under favorable conditions. Gleason⁹ has shown that to a limited extent prairie has at times replaced forest, and has described the periods since glacial time of forest advance and of forest retreat. It is readily granted that the present tendency, as well as the net trend during postglacial time, is one of very slow forest advance (very slow because after many thousands of years a goodly portion of Illinois has still not been occupied by trees). Under these conditions one may feel that forest invasion of prairie (or of now-cultivated prairie areas) is in most places hardly imminent.

Recent observations point to the probability that extensive prairie or

⁹ Gleason, H. A. The vegetational history of the Middle West. *Ann. Assoc. Am. Geogr.*, 12: 39-85, 1923.

open-field areas in Illinois which are free from the sheltering effects of forests, tree-clad towns or farmsteads, or windbreaks, have a climate which is effectively different in many respects from that of the forested areas. There are no meteorological stations in these wind-swept areas, consequently their peculiarities of evaporation, wind-movement, insolation, movement and accumulation of drifting snow, certain temperature phenomena, and possibly even of rainfall, have as yet been merely sensed. Such a station may soon be established by the College of Agriculture, University of Illinois, and the results may show that there are actually two climates in central Illinois, a forest climate and a prairie climate. The forest advance is chiefly the result of the slow reaction of upland forest upon the climate of the adjoining expanse of prairie. There need be no objection to the interpretation of this prairie which alternates with forest, as subclimax prairie (in the sense that it might eventually all come to be forested), if the possibility of another interpretation, with less emphasis on the future, be granted. It may thus be regarded as a highly developed type of prairie, less xeric than that of the Missouri river region, perhaps a climax prairie, which resists the invasion of forest to a degree. The possibility of two or more climaxes of unlike character being able to thrive within the same region, their local distribution determined by certain peculiarities of soil, drainage, or exposure, and each tending in some measure to modify its climate in a distinctive manner, ought not to be difficult to admit.¹⁰ The persistence of these separate vegetations in a diversified region may be so great as to approach a static alternation. Even in Illinois the stream-valleys and hilly areas favor forest; the poorly-drained flat uplands favor prairie. The spread of upland forest from the edge of the valley is an exceedingly slow process. A recent short paper by Godwin, with an editorial note by Tansley, discusses the subclimax concept and deflected succession.¹¹

The final paragraph of this last chapter describes the colored map of the climaxes, necessarily diagrammatic, which forms the frontispiece. Except for the difficulties of depicting narrow zones of vegetation on a small scale, the map is an excellent exposition of the views of the authors. Those ecologists who do not think in terms of climax and subclimax will be a bit surprised to note the representation of the extensive salt playas west of the Great Salt Lake as grassland, and to find extensive development of woodland or coniferous forest across the Great Basin. Sagebrush is represented about as far north as 41° latitude; north of that is grassland (the Palouse prairie). Some readers might have expected this contact to be shown farther north. It is

¹⁰ In fact, Dr. Clements himself holds this opinion. The difference in viewpoint suggested above is really much smaller than it seems. Many of the ideas expressed in "Plant Ecology" to which some readers might take decided exception, do not diverge so widely from the readers' opinion as they may seem to from the too-brief and unqualified manner of statement. This is the unfortunate result of the necessity for brevity imposed on this as upon many other texts.

¹¹ Godwin, H. The subclimax and deflected succession. *Jour. Ecology*, 17: 144-147, 1929.

explained on the basis of overgrazing which has permitted sagebrush to invade much of the original grassland. Chaparral is not separately shown, its small area not permitting it to be differentiated on the map from montane and sub-alpine forests. Woodland is also included with these. A large wall-chart permitting detailed representation of the climaxes is in preparation. [It may be that a plan of map which represents vegetation-types as overlapping, rather than each occupying an area entirely its own, would give greater flexibility and therefore closer approximation to the facts.]

The bibliography is exceedingly valuable. Six hundred and eleven publications are cited. It is evident that space limitations prevented the authors from including a number of other notable titles. References to articles is by number, and authors' names are rarely mentioned. This saves space, but is regrettable for several reasons, one of which is that students will not so readily learn to associate the names of ecological workers with their respective fields of endeavor. The manner of referring to articles, as well as to the figures, is peculiar. The reference number is at the end of a sentence or paragraph, though the phrase or sentence to which it is related may occur a number of lines above. Thus, reading on p. 448 about lodgepole pine and aspen, we come to the reference to fig. 251, which pictures a western yellow pine forest. No references are made in the text to page numbers in publications cited; only a few are given in the bibliography. This greatly reduces the usefulness of the citations to the reader.

The physical make-up of the book is without fault. The illustrations are mostly original, and are generously provided: 262 half-tones or line drawings, with the colored map of climaxes already mentioned. Those of vegetation and of root-systems are particularly good. It is to be regretted that the authors in many instances failed to give the locations in which photographs or other illustrations of vegetation were taken. Such figures as 17, 44, 51, and 232 would be of greater usefulness, especially to students, if definitely located. The index is good (18 pp.), with bold-face page references to figures. The typographical errors are very few. A few inaccuracies of plant names may be noted, as the printing of *æ* instead of *æ* in *Chamæcyparis*, *Pinus tæda*, etc. *Nuphar* is called lotus, and on p. 472 *Cercocarpus ledifolius* is inadvertently given as *Ceanothus*. A few awkward expressions occur, as the mention of roots "ramifying the soil" (p. 177), or "the volume ramified by roots" (p. 348).

The authors are to be congratulated for their able selection and organization of the enormous mass of information which the book embodies, now made generally available. The book is the most comprehensive of the few plant ecology texts in the English language. Practically every ecologist will find in it much that is new to him. It contains much more material than can be covered in a year of class work, so that selection of the topics to be emphasized in a particular course is not only possible but unavoidable. The directions for field and laboratory procedure should be particularly helpful to the

student. Two pages addressed to the teacher, concerning work in the field, precede Chapter I.

As a work of reference, "Plant Ecology" is indispensable to botanists and to all ecologists, and will prove useful to geographers, foresters, agronomists, grazing workers, and landscape architects.

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LIFE FORMS OF CONNECTICUT PLANTS¹

Statistical studies of vegetation from the standpoint of indicator significance are not new in the United States. For the most part, however, such studies have been concerned with edaphic and biotic rather than with climatic relations. For this reason Ennis' bulletin on the life forms of Connecticut plants and their significance in relation to climate is especially welcome.

By way of introduction the author summarizes rather comprehensively the life form systems developed by Humboldt, Warming, Drude, Pound and Clements, Raunkiaer, and others, and presents her reasons for adopting the Raunkiaer system in her own studies. The reviewer feels that this was an extremely wise choice; since there is little question that Raunkiaer's is the most satisfactory system of life form classification which has yet been developed. Its comparative ease of application in the field, and its general workability, are features which strongly commend it to ecologists. For that matter, any scheme of classification represents merely a means to an end—it should not be made an end in itself; it is valuable in direct proportion as it is usable.

Two applications of the life form concept in the study of vegetation are suggested, namely, (1) classification based upon consideration of the life forms of the *dominant vegetation*, and (2) classification based upon consideration of *all species* in the flora. The first is concerned with the ecological features of the dominant vegetation; the second with the ecological structure of the entire vegetation. A classification of the second type, such as Ennis uses, is especially valuable since the data can be presented statistically in the form of an ecological spectrum. Ecological spectra, representing the flora of different regions, may be readily compared. The value of the ecological spectrum as an indicator of climate is discussed at some length.

Native and naturalized species of Connecticut are recorded as to life form by families and genera in a special section. One must commend the wisdom of separating the native and naturalized plants and of indicating all evergreen species in bold face type. An idea of the task accomplished by the author is gained from the fact that 1,453 native and 169 naturalized species have been classified as to life form.

¹ Ennis, Beulah. The life forms of Connecticut plants and their significance in relation to climate. *Conn. Geol. and Natural History Survey, Bull.* 43, pp. 1–100, 20 pls., 1928.

Perhaps the most interesting section of the bulletin is that in which the Connecticut flora and climate are compared with the flora and climate of other regions in eastern North America. The data broadly indicate that Connecticut, in common with Mississippi, Alabama, Cape Breton, and Iowa, is a region characterized by a preponderance of hemicryptophytes and having a cold season of sufficient intensity to cause suspension of growth. A more critical study of the data, particularly that dealing with the arborescent phanerophytes, indicates quite clearly that Connecticut lies in the transition zone between the region favorable for the development of broad-leaved evergreen species (Alabama and Mississippi) and the region most favorable for the development of conifers (Cape Breton). It is thus apparent that climatic conditions, not only in their broader aspects, but also their more local phases, may be inferred from careful study of life forms. This is a field of interesting possibilities. It may be that the data supplied by such studies could be profitably supplemented by critical examination of the seasonal annulation of woody stems, and perhaps other peculiarities of growth, in the different regions.

The author reaches the conclusion on p. 91 that, "the ecological climax of this region [Connecticut] is deciduous forest with an element of conifers." It is the reviewer's opinion, based on work² in the same region, that the coniferous element, which Ennis implies is of lesser importance, is dominant in the climatic climax stands. It seems dangerous to attempt to draw conclusions as to the climax vegetation of a region solely on the basis of the life forms now present.

A few typographical errors occur. In the bibliography the place of publication of Nichols' paper³ is not indicated. In Section III, "List of the species in the Connecticut flora arranged by families and genera and tabulated according to life form," certain values are included in parentheses, but their significance is not indicated. Presumably they represent numbers of genera and species of naturalized plants in the various life form classes. The source of Plate 1, which was apparently copied from Raunkiaer, failed to be acknowledged.

The plates are excellent, and the plants selected to illustrate various life forms are well chosen. Everything considered, Ennis' paper is unquestionably the best exposition of Raunkiaer's system which has yet appeared in this country. The bulletin is one which merits the widespread attention of plant ecologists, particularly those interested in the significance of life form in relation to climate.

Copies can be secured upon application to the State Librarian, Hartford, Connecticut.

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² Lutz, Harold J. Trends and silvicultural significance of upland forest successions in southern New England. *Yale University: School of Forestry, Bull.* 22, 1928.

³ Nichols, G. E. A working basis for the ecological classification of plant communities. *Ecology*, 4: 11-23, 154-179. 1923.

FIELD BOOK OF PONDS AND STREAMS¹

This "Field Book of Ponds and Streams" by Professor Ann Morgan of Mt. Holyoke College attempts the difficult task of introducing the interested amateur to the life of ponds and streams which Lutz successfully performed for insects in general in his Field Book of Insects, one of the earlier volumes in the present series. The general appearance will be familiar to those who have pleasantly increased their knowledge of insect life under the stimulating guidance furnished by Lutz. The present field book begins with three introductory chapters, one of which deals briefly with the main features of the water environment and includes a 3-page long, partially pictorial key to aquatic plants and animals; another summarizes the life in ponds and streams and the third deals with simple apparatus and methods for collecting, observing and preserving water animals.

Sixteen chapters make up the main body of the presentation as follows: simpler plants and animals; higher plants; sponges; the Hydras, bryozoans; thread worms; leeches; crustaceans; water mites; aquatic insects; snails and mussels; lampreys and fishes; salamanders, frogs and toads found in or near water; turtles and snakes found in or near water. These are followed by a bibliography of 18 pages including 11 general titles and a brief list of references for each chapter. The chapter bibliographies include taxonomic and natural history references. A 5-page glossary and a full index complete the presentation.

The charm of water life with its simplicities and its intricacies are opened to the student without over-statement or effort for effect. The main body of the discussion is taken up with facts and with simplified keys which should enable the observer to approximate identification and may lead him on to the more inclusive keys of Pratt and of Ward and Whipple, just as these latter should send the careful student to the monographic special literature and museum collections for final determination. The introductory general key is, unfortunately too condensed and the figures are too small to prove most helpful to the uninitiated student.

The reviewer's reaction to this volume has run from pleasant anticipation based on advance information through acute disappointment on first inspection, to reassurance on more careful reading. The disappointment was due to the brevity of treatment of many of the groups. For example, from all of the fresh water Protozoa, only the following are mentioned: *Stentor*, *Spirostomum*, *Paramoecium*, *Vorticella*, *Epistylis*, and *Charchesium*. The first five are figured. The complete discussion of the last three follows:

"Colonies of *Vorticella* or *Epistylis* make the fluffy whitish patches which can be found in summer and winter on the bodies of water-insects and crustaceans, or on submerged sticks and stones. In some streams scarcely an insect

¹ Morgan, Ann Haven. Field Book of Ponds and Streams. An introduction to the life of fresh water. New York and London, G. P. Putnam's Sons. 448 pp.; 10 x 17 cm.; 300 line cuts; 15 illustrations in black and white, and 8 in color. 1930. \$3.50.

will be found which does not have a crop of these springing, bell-like animals growing upon it. Colonies of *Charchesium* are common on the undersides of sticks and stones in streams, where they grow nearly an eighth of an inch high." The criterion for selecting these forms for mention is that "either singly or in clusters they are large enough to be seen through a hand lens, sometimes even with the naked eye."

The student of fishes will be chagrined to find that this group receives only half the space given to "Salamanders, frogs and toads found in or near water," a situation which a specialist in the latter group explains as being due to the greater inherent amateur interest in the amphibians.

My own reassurance came from the fact that closer attention revealed a generally consistent sweep of emphasis through the different groups of water animals, and from the realization that what I really desire is a set of books on the life of fresh waters of the present size with separate volumes dealing with the Protozoa; the lower metazoans including the Vermes; molluscs; insects; fishes; and finally, one dealing with fresh water herpetology. The present volume should serve merely as the introduction to these more specialized field books.

In conclusion I wish to quote with approval the final paragraph of Professor Needham's brief foreword: "A book like this cannot fail to render good service since it tells the simple truth about aquatic creatures in an interesting way, illustrates them with good figures, and so enables the reader to know what they are like and where to find them."

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NOTES AND COMMENT

MEASUREMENT OF LIGHT BY THERMOPILES

Some time ago the author¹ published a paper in which the assumption was made that the amount of visible and ultra-violet light on a very clear day was nearly a constant fraction of the total solar radiation. This assumption was based on numerous readings. Perhaps because of this, others have assumed that such is always the case. On days which might be classified as "hazy" the amount of light in solar radiation varies from 40 per cent to 70 per cent of the total solar radiation. Radiation from an electric light bulb is about 14 per cent visible light. From an ecologist's point of view it would seem that it is the light and not the total radiation which is important. A thermopile will measure light alone only when the infra-red radiation is absorbed previously by water. Thermopiles of the type described by Shirley² and Gast³ do not permit this.

A thermopile, mounted on an equatorial mounting, and used in conjunction with a water filter and color filters, where desired, gives an accurate method of measuring any part of the solar spectrum. In comparing different parts of spectrum it should be remembered that the readings of the thermopile in calories should be divided by the calories per quantum for the particular wave length of light measured. Various attempts have been made to construct a thermopile which will measure light from all directions. To accomplish this the absorbing surface must be spherical, which renders the filtering out of infra-red radiation by water almost impossible. A flat surface thermopile, when kept in a horizontal position, gives a very poor measurement of solar radiation since it presents no surface to the sun at sunrise and an increasing area, and still more rapidly decreasing per cent of reflection, as the sun becomes higher in the sky. On a very clear day thermopiles mounted in this manner give readings which gradually increase from sunrise to noon, whereas the sunlight reaches from 70 per cent to 90 per cent of its full value immediately after sunrise, and increases to almost its full value in about 3 hours.

A more complete discussion of this type of measurements has been given previously.⁴

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SOME COHABITANTS OF BURROWING CRAYFISH

During the course of a zoological expedition in the Missouri Ozark Mountains this past summer the writer, in company with Mr. E. B. Williamson, dug some specimens of *Cambarus diogenes* from their burrows. The specimens were obtained in a dried slough adjacent to the Current River about 2 miles south of Van Buren, Carter County, Missouri. During high water the slough is flooded by backwater from the river. The water level on August 27, 1930, was reached after digging through about 3 feet of hard clay.

¹ Burns, G. Richard. Studies in tolerance of New England forest trees, VI. A portable instrument for measuring solar radiation in forests. *Vt. Agr. Exp. Sta. Bull.* 261, 1927.

² Shirley, H. L. A thermoelectric radiometer for ecological use on land and in water. *Ecology*, 11: 61-71, 1930.

³ Gast, P. R. A thermoelectric radiometer for silvical research. *Harvard Forest Bull.* 14, 1930.

⁴ *Loc. cit.*, footnote 1.

After the infuriated crayfish had been extracted a great many smaller crustaceans were seen in the pocket of the burrow. Examination disclosed the presence of ostracods, copepods, and amphipods in great abundance. A quart of water was taken back to camp, and, after the mud had settled, the animals were collected and preserved. More than 6,000 specimens were obtained as estimated by a count, and many, no doubt, were lost in collecting due to the crude methods employed. Of the 3 species obtained in the burrow the ostracods were by far the most numerous. Most of the amphipods were immature but no nauplii of the copepod were obtained.

The identification of the specimens obtained is as follows: Ostracoda, *Cypria exsculpta* Fischer; Copepoda, *Osphranticum labronectum* Forbes (determined by Dr. Stillman Wright); Amphipoda, *Eucrangonyx gracilis* (Smith). The ostracod is reported as very common and world wide in distribution. *Osphranticum labronectum* is found widely distributed throughout the United States, and occurs as far south as Guatemala. *Eucrangonyx gracilis* has been reported previously from Michigan, Wisconsin, Illinois, Ohio, Tennessee, New York, Virginia and Ontario.

If the cohabitation of crayfish burrows by other crustaceans is at all common, the rate of reestablishment of a fauna in a temporary pond may be directly related to the number of crayfish burrows present.

The establishment of a subterranean crustacean fauna might well be effected occasionally by means of crayfish burrows, which sometimes extend to a depth greater than 6 feet below the surface, and sometimes into underground and flowing water channels.

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NOTES ON PREDICTING THE PROBABLE FUTURE DISTRIBUTION OF INTRODUCED INSECTS ¹

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The climatic analysis of insect distribution is a new field, and the methods involved have been worked out only in a crude fashion. However, it seems a promising field, and one in which advances are certain to be made in the near future. For this reason it seems advisable to make a few statements regarding the technique which has been used by the writer and his students, and regarding the possibilities and limitations of such studies.

In a general way, everyone admits that the distribution of plants and animals is controlled by climatic conditions, and that the climate is the basic factor underlying all living associations. Also, in a general way, most biologists will admit that the distribution of any single organism is governed by climatic conditions. But when the statement is made, for example, that the northern distribution of the San Jose scale is limited by the occurrence of certain fatal winter temperatures, the agreement is not so general. Most workers require very rigid proof of this or of any similar statement. To proceed further, and predict the distributional limits of an insect in several directions, as determined by several different climatic factors, is deemed very hazardous. This is not necessarily the case, for this procedure may be perfectly sound, and of great value as a groundwork for future studies.

The methods which have been evolved in the course of several such studies are rather simple, but require care in the interpretation of findings. The principle involved is that of comparison of environments. When an insect like the Mediterranean fruit fly is found in Florida, it is of great interest to determine its probable spread, and the places in which it will cause the greatest damage if introduced. If a careful comparison is made between those environments where it is now abundant and destructive, and those in America into which it might enter, it is possible to secure a tentative answer to these questions.

¹ Contribution from the Entomology Department, Montana Agricultural Experiment Station.

The point is missed if it is assumed that an intimate knowledge of the physiology and habits of the insect is essential. The method simply takes the known distributional facts, studies them in relation to climatic limitations, and applies those limitations to the new area under consideration. It makes the basic assumption that the distribution is limited by climatic conditions, and proceeds to discover what those limitations are at present. Assuming that they will be unchanged in the new area, it is then possible to map the future distribution. It is not necessary to know whether the climatic factors finally selected operate directly upon the insect or indirectly upon its parasites and predators, for the final result will be the same in either case.

The method involves:

1. The collection of data regarding the distribution of the insect in its present habitats, together with data regarding the severity of infestation in the various habitats.
2. The sorting of these data into categories representing roughly three degrees of damage, which correspond to the three zones of distribution which I have outlined elsewhere (Cook, '29).
3. The collection and plotting of climatic data from all of these habitats, both retaining the original data and combining them to form average charts for the three degrees of severity.
4. The careful study of these charts to determine the limiting climatic factors. The climatic limitations are not always evident, but in most cases the average data for the three zones of abundance will line up in such a manner as to indicate them. Mr. Gjullin ('31) has shown this very clearly for the Mediterranean fruit fly.
5. The collection and study of any physiological data that are available, in order to check the findings of the climatic study.
6. The comparison of the favorable and unfavorable climates in the present distribution of the insect with the climate of the new area under consideration.
7. The preparation of a map showing these climates in the new area, and predicting the probable future distribution and relative severity of infestation.

It will be seen that the method involves no original study of the insect itself, although, if opportunity arises, the climatic study should be checked by careful physiological studies. Two sorts of data are involved, climatic and distributional, and the accuracy of the final forecast depends upon the accuracy of these data. The prediction will be reliable in so far as the basic data are accurate, but no farther. The distributional data are usually rather unsatisfactory, in that it is difficult to estimate the relative intensity of infestation in various parts of the present habitat; so this is usually the weakest part of the study. Even with rather incomplete data, however, it is possible to predict the future distribution with a fair degree of accuracy. The isolated facts procured from many sources will be found to fit together and produce a picture of the climatic limitations.

In this connection it seems fair to point out the degree of success obtained in two earlier attempts to predict the distribution of injurious insects. In January, 1924, I outlined the regions in the United States in which outbreaks of the pale western cutworm might be expected (Cook, '24). At that time it had been reported from Alberta, Montana, North Dakota and Colorado. Since then, other outbreaks have occurred in the original area, and in addition one in northeastern New Mexico and one in extreme western Oklahoma, both of which areas were included in the economic distribution on the original map. In March, 1925, another paper (Cook, '25) was published in which I attempted to predict the future economic distribution of the alfalfa weevil. This study was based entirely upon published data. Up to the present time only one or two small colonies of the weevil have been found outside the areas outlined on my map, and no commercial damage has been done. In several instances the weevil has spread to the boundaries as indicated on the map, and has not crossed them.

This method will not give the absolute distribution of an insect, as the climatic data are not sufficiently detailed, and it is obviously impossible to show all places where a favorable variation may produce a small habitat outside the general limits; but it will give the economic distribution with considerable accuracy, and that is the point of greatest practical interest.

The usefulness of the method is evident. Once the reliability of such a study is well established, it may be used upon insects which are just gaining a foothold on our shores, as a basis for intelligent quarantines, which will not hinder commerce between the infested area and those regions where no damage is expected. There is no use in maintaining a quarantine against an insect that would do very little damage if introduced, and the energy used in enforcing such quarantines might well be applied to the more rigid enforcement of those against insects that would be really dangerous if they obtained a foothold.

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PROBABLE DISTRIBUTION OF THE MEDITERRANEAN FRUIT FLY (*CERATITIS CAPITATA* WEID.) IN THE UNITED STATES¹

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The Mediterranean fruit fly has recently become established in Florida, and is costing the State and Federal Governments large sums of money in their effort to eradicate it. It is also preventing the marketing of fruit from some localities due to the quarantine restrictions which have been placed on certain districts to prevent its further spread. There is always the possibility that it may slip through the quarantine inspection in Florida or that it may get through from some of the other countries where it occurs, and so establish itself in new areas. In view of these facts, it would be of considerable interest and importance to establish with some degree of accuracy its probable distribution in the United States and the extent to which damage might be expected in the different regions. This paper is an attempt to determine such distribution and damage.

The more important available data on the effect of temperature, rainfall and humidity on the fruit fly will first be presented. A climatological study will be made of all known occurrences of the fruit fly in the different parts of the world, to determine the optimum and limiting conditions. This information will then be used in a study of climatic conditions in the United States to determine the limits of probable distribution and to locate those areas having optimum conditions. The method of climatic analysis will be much the same as that used by Cook ('25).

LIFE HISTORY

The eggs are laid just below the surface of the skin of the fruit. Here they hatch in from 2 to 6 days under favorable conditions. The larvae feed throughout the pulp of the fruit, and, under favorable conditions, complete this stage and emerge in from 6 to 10 days. They burrow into the ground to pupate and the adults emerge in from 20 to 28 days. The adults live an average of 6 to 10 weeks. Under favorable conditions the length of the egg, larval and pupal stages may be much increased. With unfavorable food and temperature conditions, the life of the adult female may be shortened, while with unfavorable ovipositing conditions it may be prolonged.

¹ Contributed from the Department of Entomology, Montana State College, Bozeman. Presented as a thesis in the author's work for the Bachelor of Science Degree in Entomology. Mr. Gjullin was guided in his thesis by Doctor W. C. Cook of the Department staff. Published with the approval of the Director of the Montana Experiment Station.

CLIMATIC CONDITIONS AFFECTING LIFE HISTORY

Temperature

Of the effect of temperature on the egg, Back and Pemberton ('18, p. 49) found that:

"All of 131 eggs one day old when placed at Puulehau, where the temperature ranged between 39° and 89° F., with a mean of about 52° F., were still unhatched after 16 days at Puulehau, after which they were taken to Kealekakua, where they hatched the following day or when 18 days old.

"Eggs deposited during a 4-hour period were placed immediately at 49° to 56° F.; after refrigeration for 21 days 1 living and 7 recently dead first-instar larvae and 51 unhatched eggs were found. Of other eggs deposited at the same time but held at normal temperature for from 44 to 47 hours before being placed in storage, 8, 12 and 48 had hatched after refrigeration for 16, 19 and 21 days. One egg, 2 days after deposition, was held in storage at a temperature of from 40° to 45° F. for 20 days when it was removed to normal temperature where it hatched three days later, or 25 days after deposition. One egg placed at 25° to 30° F. when 1 day old and held at this temperature for 7 days, hatched 3 days after removal, or 11 days after deposition."

Berro ('26) found that when grapes from Almeria, Spain, were placed in cold storage for 14 days in crossing the Atlantic at a temperature of 29.3° F., with a maximum of 32° F., all eggs and larvae were destroyed in grapes packed in cork dust. Pupae placed at a temperature of 35.78° F., never rising above 38.3° F., were also destroyed in 14 days.

Back and Pemberton ('16, p. 125), after extensive experiments, found: ". . . That no eggs or larvae survive refrigeration for 7 weeks at 40° to 45° F., for 3 weeks at 33° to 40° F., or for 2 weeks at 32° to 33° F."

These experiments seem to indicate that the loss of a certain number of heat units is necessary to cause the destruction of eggs or larvae, and that unless enough heat units are lost to cause such destruction, the lowering of temperature does not materially lengthen the time required except as it tends to retard the accumulation of the heat units necessary for the completion of these stages.

In regard to optimum and limiting temperatures Back and Pemberton ('18, p. 78) say:

". . . Development appears to progress most rapidly after the Hawaiian temperature mean reaches 75° or 76° F. At a mean of 68° F. the developmental period is about doubled. A temperature ranging between 58° and 62° F. has no detrimental effect upon the development as shown by the emergence of adults from pupae in a well lighted refrigerator. . . . All cold storage data obtained by the writers indicate that approximately 50° F. is the temperature at which little or no development can take place and below which complete mortality occurs if exposures are continued sufficiently long."

There is considerable mortality among larvae in fallen fruit which lies in direct sunlight. Back and Pemberton ('18, p. 77) found that:

"The larvae within fruits which lie in direct sunlight after they have fallen, are killed in large numbers. Often all larvae in the portion of the fruit exposed to the sun

will be found dead. During August, 1914, mangoes were exposed to the sun for two days over sand in shallow trays. Examination later proved the 17 fruits to contain 17 living and 84 dead third-instar larvae with 14 larvae dead on the surface of the fruit. One larva died when partly out of the fruit and 103 succeeded in pupating normally. In 23 other fruits held in the shade as a check, there were found 168 living and 9 dead third-instar larvae and beneath them 167 pupae. While every larva in certain fruits exposed to the sun was killed, it is evident that many larvae in the protected portion of the fruit may escape and pupate."

In regard to the effect of temperature on the pupal stage, Back and Pemberton ('16, p. 257) found that:

"Temperatures ranging between 49° and 51° F. and averaging about 50° proved most interesting of all, as these appear to be very close to the point below which the insects' activities cease. This temperature was secured by use of an ordinary refrigerator 42 x 34 x 18 inches. During the period from May to July, 1914, 31,700 pupae were used in an experiment to determine the effect of this temperature upon pupal development. Pupae in 15 lots, of ages ranging from 1 to 8 days and averaging 3,523 pupae for each of the 8 days represented, were held in storage for 2 months before being removed. Frequent observations were made but no pupae completed their development and yielded adults in storage. On removal to normal temperatures all of the 31,700 pupae were found dead."

Of the length of the pupal stage, Back and Pemberton ('18, pp. 60-61) say:

"While it is probable that the duration of the pupal stage in any fruit-growing section in Hawaii is never more than 20 to 28 days (average mean temperature of 66.8° F.), the writers have shown that it may be much longer under colder conditions."

The longest period obtained for pupal development by them was 60 days.

The adult fly is not a factor in carrying the insect through adverse climatic conditions. Back and Pemberton ('15, p. 327) write:

"... Mr. George Compere reports having seen adults sunning themselves on orange trees in Spain after a night during which the temperature dropped to freezing, thus showing that adults can withstand temporarily any cold snap likely to occur in a citrus section. However, the fact that the adults do not succeed in thriving during the winter temperatures of Southern Spain and Italy and in Sicily, seems to be well proved by the fact that it is only during the summer and early fall that the fruit fly becomes a serious pest in favored host fruits and in over-ripe citrus fruits. If this were not so, fruits would become badly infested much earlier in the season than they do. The number of adults surviving the winter must be very small. Even the mild winters of Hawaii at Honolulu have a very noticeable effect upon the numerical abundance of adult flies, as shown by two experiments extending over one full year."

Of the influence of temperature conditions on oviposition, Back and Pemberton ('18, p. 74) say:

"No satisfactory data on this subject can be secured out-of-doors in the Hawaiian Islands, as the colder temperatures which seriously affect adult activities are not to be had except at higher altitudes, where the fly is not to be found. At Volcano House, Hawaii, at about 4000 ft. elevation, where the November mean is about 60° F. and the daily mean is between 45° and 72° F., adults in jars were inactive during early morning

and late afternoon. During the warmer period of the day adults became active and oviposited in apples hung in their jars after the temperature reached 61° F. At Honolulu, at temperatures of 65° to 67° F., 27 eggs were deposited in peaches by about 40 females, and 40 eggs by a lot of 60 females. At higher temperatures many more eggs would have been deposited under otherwise similar conditions. Adults in jars were noted to mate as usual on March 17, when the temperature was 69° F. On March 18, 9 A.M., at 67° F. adults endeavored to oviposit in apples but did not seem to succeed in puncturing the skin. A female emerging on August 12, 1914, was placed in a large glass refrigerator the temperature of which averaged 61° F., but varied for the period between 58° and 62° F. She was accompanied by mates and deposited eggs on September 12 and 20 respectively but died on September 25. This fly was replaced by another of like age, which deposited 9, 5, 8, 4, and 6 eggs, respectively, on September 26, 27, 28, 29, and October 2."

Rainfall

A large amount of rainfall in the colder months of the year appears to be a limiting factor in pupal development. Back and Pemberton ('18, p. 80) say:

"Newman in Western Australia has found that a very large percentage of pupae are killed by a cold, wet winter when the ground is frequently flooded. Such conditions so lessen the abundance of the fruit fly that there are relatively few flies, numerically speaking, to infest the early fruits of the succeeding season. On the other hand, unusually severe outbreaks of the pest in both South Africa and Australia have been attributed to exceptionally dry, mild winters which make it possible for many adults to be present the following spring to start early summer generations. . . ."

Of the effects of varying humidities on the different stages, no information is available.

SUMMARY OF CLIMATOLOGICAL EFFECTS

Development appears to progress most rapidly at a mean temperature of 75° or 76° F. Below this mean temperature, development gradually slows down. Below 50° F. mortality occurs if exposures are continued long enough. No eggs, larvae or pupae survive temperatures of 32° to 33° F. for over two weeks.

Oviposition is known to occur at temperatures as low as 61° F.

Large numbers of larvae are killed at ordinary temperatures if the fallen fruit is allowed to lie in direct sunlight.

Cold, wet winters are a limiting factor in the pupal stage while dry, mild winters, such as are found in South Africa, form a favorable environment.

CLIMATE OF COUNTRIES IN WHICH *CERATITIS CAPITATA* IS KNOWN TO OCCUR

Data concerning the distribution and severity of *Ceratitis capitata* were obtained from Back and Pemberton ('18, pp. 3-9) and by a systematic survey of the abstracts of all articles pertaining to the Mediterranean fruit fly to be found in the volumes of the Review of Applied Entomology, Series A, and

the volumes of the U. S. Department of Agriculture Experiment Station Record. The map (Fig. 1) shows the approximate distribution and severity as determined from these sources.

In studying the climate of infested regions, climographs, based on the composite mean temperature and rainfall of the region, were used as a means of comparison. Climatological data were obtained from Kendrew ('22) and Hann ('08-'11). In no case were the temperature and rainfall of any one station taken as the basis for the climate of a region.

Serious infestations of the fruit fly occur in the Hawaiian Islands and the Union of South Africa. Climographs for these places are shown in figures 2, 3, 4, and 5.

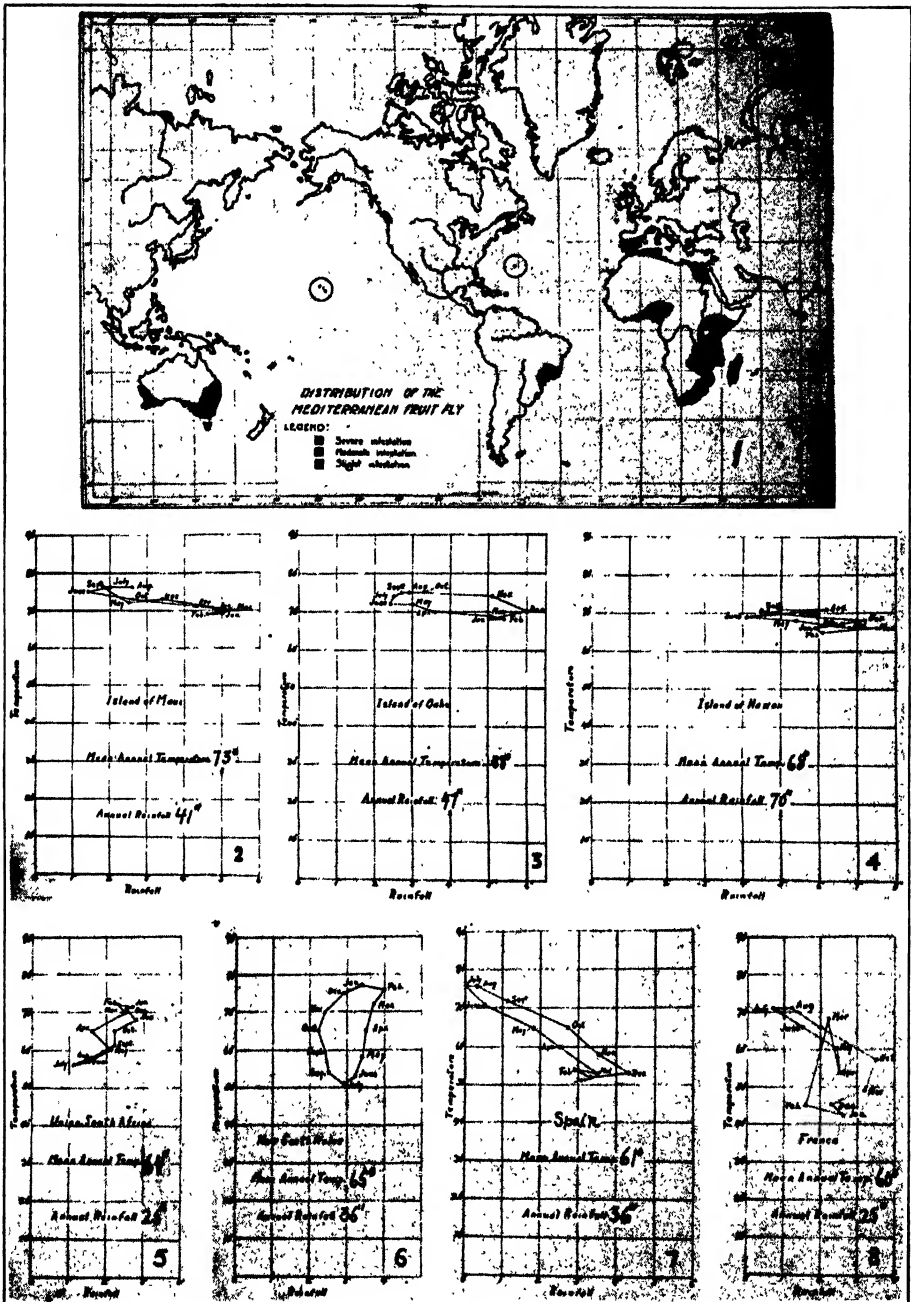
The stations given by Back and Pemberton ('18, p. 10) as being representative of the variations in the range of temperature at the respective elevations of points in the Hawaiian Islands where the host fruits are grown, were taken as a basis for the climographs in figures 2, 3 and 4. For the three islands, yearly mean temperature of 72° F. that varies between the monthly means of 65.9° and 76.6° F., with a mean annual rainfall of 53.6 inches, produces a climate in which development is only slightly retarded during the colder months. This climate produces as high as 15 or 16 generations per year.

In the fruit growing sections of South Africa, the dry winter months and temperatures which do not go below a monthly mean of 56° F. explain why serious infestations may occur in spite of temperatures that are below 65° F. for 5 months of the year and temperatures which do not exceed a monthly mean of 72° F. for the rest of the year. The climograph in figure 5 is a composite graph of stations located at Graaf Reinet, Cape Town, Port Elizabeth, Durban, and Pretoria.

A medium infestation of the fruit fly occurs in New South Wales. A mean monthly temperature which is below 65° for 6 months of the year and which reaches a low of 51° mean temperature for July, is the important limiting factor which retards development. Averages of temperature and rainfall from Sydney, Port MacQuarrie, Bourke and Dubbo were used as a basis for the climograph in figure 6.

Climographs for Spain and France are typical of two somewhat different climates, both of which have a slight infestation of the fruit fly. The large amount of winter rainfall in Spain tends to produce the same effect on the overwintering pupae as the considerably lower winter temperatures of France.

The rainfall in Spain varies between 4 and 5 inches during the coldest months of the year. This, in combination with a temperature which reaches a low monthly mean of 53° F., is perhaps the main reason for the small amount of damage to fruit in Spain as compared to the damage in South Africa. The climograph (Fig. 7) does not give a true indication of moisture conditions during the summer months, since irrigation here supplants rainfall. Data from stations at Lisbon, Gibraltar and Seville were used for the graph (Fig. 7).



FIGS. 1-8. 1. The present distribution of the Mediterranean Fruit Fly. 2, 3, 4 and 5. Climographs for areas having severe infestation. 6. Climograph for New South Wales where medium infestation occurs. 7 and 8. Climographs for countries having slight infestation.

Middleton ('14) records the fly as having been imported into England as far back as 1868 in oranges used in making marmalade. There is but one record of fruit in England producing the fly.

France, therefore, marks the northern limit of fruit fly infestation. The climograph (Fig. 8) is a composite graph for Paris, Perpignan, Menton, Montpellier and Cannes. For about 7 months of the year the mean monthly temperature is below 65° F., and for more than 3 months it is below 50° F. This, combined with a rainfall varying from 1.5 to 3 inches kills a large percentage of the larvae. Here, as in Spain, irrigation supplants the low summer rainfall. The fly maintains itself and does some damage in the neighborhood of Paris. The mean temperature here for the 3 coldest months is less than 38° F. There is very little precipitation during these months, however, and it is probable that under wet conditions the pupae and larvae would be destroyed at these temperatures.

SUMMARY OF THE EFFECT OF CLIMATIC CONDITIONS IN ALL INFESTED AREAS

In a study of this material and further extensive studies of other infested areas for which no climographs are presented, the limiting factors appear to be a mean temperature of less than 35° F. for 3 months of the year, combined with not less than 2 inches of precipitation per month.

A large amount of rainfall during the winter months is equivalent in effect to lower temperatures.

Favorable conditions are temperatures between 70° and 80° F. combined with a monthly rainfall of from 3 to 7 inches.

THE FRUIT FLY IN THE UNITED STATES

If the temperature is favorable the fruit fly may be expected to occur in those sections of the country where rainfall and irrigation produce sufficient moisture for the growing of fruit crops.

Irrigation is practiced in many areas which would otherwise not be able to grow fruit. This irrigation, however, is carried on mostly during the growing season and will not be a factor of control in combination with low winter temperatures.

The pupa of the fruit fly overwinters in the soil. Mean air temperatures were used in determining the probable distribution of the fruit fly in the United States. It was therefore necessary to determine how the air temperature varied with the soil temperature at a depth of from 1 to 3 inches, at or near the limiting temperatures for the pupa.

Unpublished data secured in Minnesota by Mr. G. A. Mail show that at air temperatures from 30° to 38° F. the soil temperatures in the first few inches have about the same mean values as the air temperatures. There is a fluctuation in the air temperature of about 5 degrees above and below the

soil temperatures. Since soil and air temperatures are very nearly the same at the temperature which limits overwintering larvae, the mean air temperatures were used in determining the limits of probable distribution of the fruit fly.

The map, figure 9, shows the climatic distribution of the Mediterranean fruit fly in the United States. It is based on the material that has been presented in this paper and on data taken from Ward ('25), the U. S. Department of Agriculture Weather Bureau, Atlas of American Agriculture (U. S. Dept. Agr., '22), and Irrigation, Fourteenth Census (U. S. Dept. of Commerce, '20).

The zones of normal, occasional, and possible abundance have been defined by Cook ('29, p. 289) as follows:

"The zone of normal abundance is by definition a zone within which limiting conditions rarely or never occur.

"The zone of occasional abundance is by definition a zone within which the insect is held down to small numbers by climatic conditions and only occasionally is able to rise to destructive numbers.

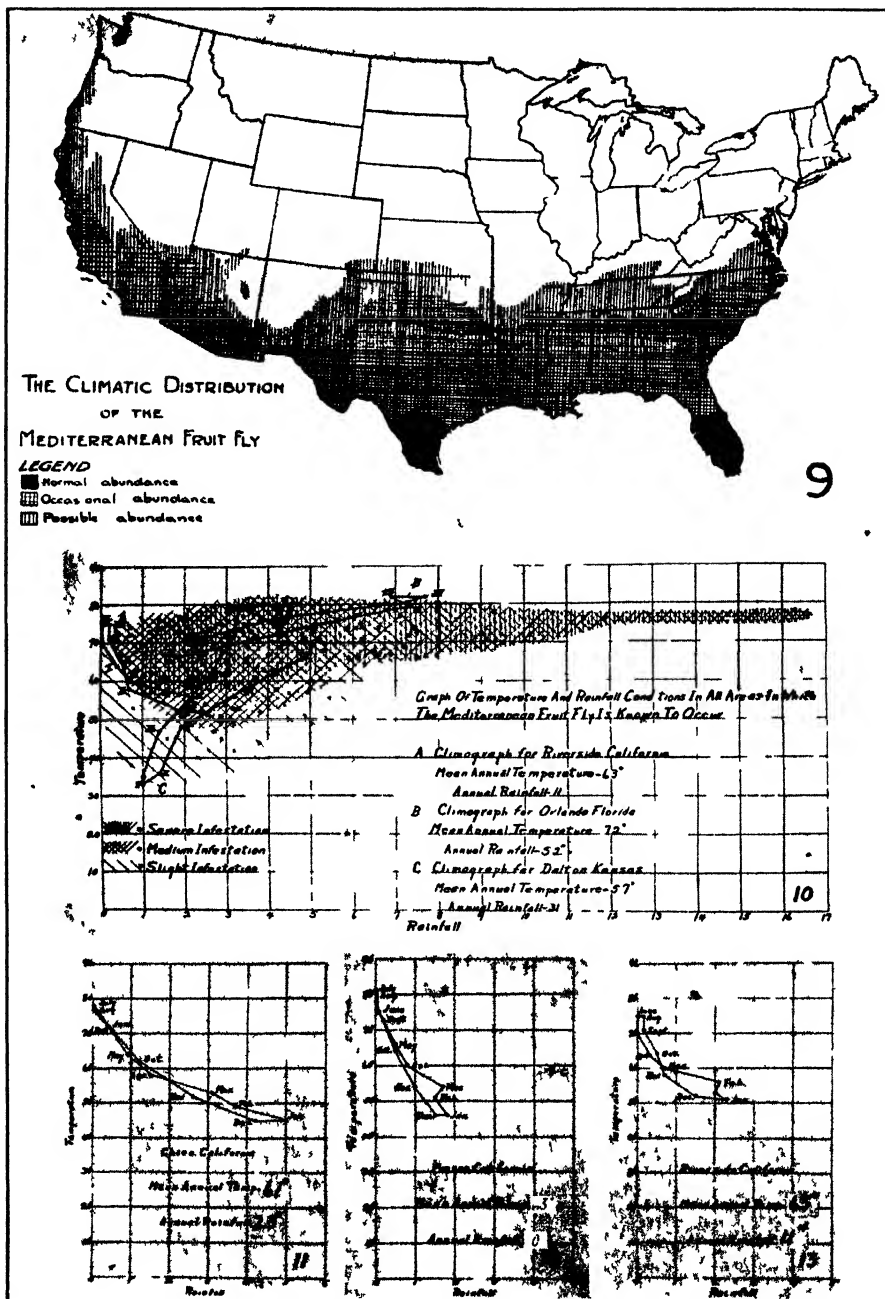
"The zone of possible abundance includes all areas not within the other two zones in which it is climatically possible for outbreaks to occur. The normal climate of this zone is such that the insect cannot maintain a permanent population but it may move into this region during outbreaks in parts of the inner zones and produce a large enough population to cause severe damage before it is checked by return to the normal climate."

The limits of the zone of normal abundance, as shown in the map, are a mean monthly temperature of not less than 60° F. in combination with heavy rainfall during December, January and February, and a mean monthly temperature of not less than 55° F. in areas where precipitation for December, January and February does not exceed 5 inches.

The limits of the zone of occasional abundance as shown are a mean monthly temperature of not less than 37° F. in combination with rainfall which does not exceed 5 inches for December, January and February. In regions having over 5 inches of rainfall the temperature varies upward in proportion to 42° F.

Limits of the zone of possible abundance are a mean monthly temperature varying from 30° F. to 35° F. in proportion to the precipitation during the months of December, January and February. Areas with mean monthly temperature of 30° F. have less than 5 inches of precipitation during these months.

In figure 10 climographs for Orlando, Florida; Dalton, Kansas, and Riverside, California, have been superimposed on a background showing the temperature and rainfall conditions in all areas in which the fly is known to occur. Data for the graph are based on the regions of severe, medium and slight infestation, as shown in figure 1, and the points as shown in the figure are the average of the mean monthly temperature and rainfall of several stations in each area. The graph is intended to show roughly the climatic



FIGS. 9-13. 9. The probable distribution of the Mediterranean Fruit Fly in the United States. 10. Climograph on background showing climatic conditions in all areas in which the Mediterranean Fruit Fly occurs. The climograph for Orlando, Florida, is typical of conditions under which a "Normal Abundance" of the Fly would occur, and the climograph for Dalton, Kansas, is typical of conditions under which a "Possible Abundance" might occur in figure 9. 11-13. Climographs typical of conditions in Northern, Central and Southern California respectively.

conditions in areas having different degrees of infestation. In many cases the climate is much the same in these areas during parts of the year, and infestations are the chief difference, as the graph shows.

The climograph for Orlando, Florida, indicates that fruit fly infestation here may be expected to be severe. It falls within the severe area as shown by the graph. Nearly optimum temperature and rainfall conditions exist for 7 months of the year. The mean winter temperature is above 60° F., and there is comparatively little precipitation during the winter months.

The climograph for Dalton, Kansas, is typical of areas within the possible zone, figure 9, in which outbreaks might occur if climatic conditions varied considerably from normal.

Climographs, figures 11, 12 and 13, for Chico, Fresno and Riverside respectively, were taken as being typical of existing conditions in Northern, Central and Southern fruit growing sections of California. Orchards are irrigated in spring and summer.

In the southern part of California irrigation tends to produce almost optimum climatic conditions. The mean monthly temperature does not go below 50° F. and winter precipitation is slight. Serious infestation may therefore be expected.

In the central part, rainfall varies considerably but is only slightly greater in the winter months than in the southern part. The winter temperature averages about 5 degrees cooler in this section, however, and this will tend to slow down development somewhat so that infestations here will not be as serious as those farther south.

In the northern part of California the high winter rainfall, combined with low temperatures, should kill many of the pupae and check the remainder so that infestation should not be serious.

Heavy winter rainfall, such as occurs in Alabama, Mississippi, and in portions of states adjoining them, will undoubtedly be an important factor in reducing the overwintering population of the fly in this region.

The sequence of host fruits is an important factor in determining the abundance of the fruit fly. There is little doubt that this factor may cause a wide variation in the population of the fruit fly within the zones as they are outlined.

SUMMARY

The more important available data on the effect of temperature, rainfall, and humidity on the life history of the fruit fly have been presented.

A climatological study of all known occurrences of the fruit fly in the different parts of the world has been made to determine optimum and limiting conditions.

A study of these occurrences indicates that if the Mediterranean fruit fly is allowed to spread, severe infestations may be expected in southern Florida and southern Texas.

In the greater portion of the fruit growing sections where this insect can maintain itself, it would cause a medium infestation. Within this zone it would be held down to small numbers by climatic conditions, and only occasionally would large populations of the fly be produced. Portions of Oregon, California, Nevada, Arizona, New Mexico, Texas, Oklahoma, Arkansas, Mississippi, Alabama, Georgia, Florida, South Carolina and North Carolina, and all of Louisiana would be included in this zone.

Beyond this zone of "occasional abundance" is a narrower zone of "possible abundance." Within this zone the insect cannot maintain a permanent population, but under favorable conditions it may cause outbreaks. Portions of Washington, Oregon, California, Nevada, Arizona, New Mexico, Texas, Colorado, Oklahoma, Arkansas, Tennessee, Kentucky, North Carolina and Virginia would be included in this zone.

I wish to thank Dr. W. C. Cook for his advice and encouragement in the preparation of this paper, and Dr. Filippo Silvestri for his valuable criticism of the map in figure 1 showing the distribution of the Mediterranean fruit fly.

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DEVELOPMENT OF ROOTS AND SHOOTS OF CERTAIN DECIDUOUS TREE SEEDLINGS IN DIFFERENT FOREST SITES

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This investigation deals with the activities of 5 species of deciduous forest-tree seedlings. Each species was grown in 3 habitats, including the one in which it naturally occurs. The study includes the development of both roots and tops during the first 3 years; measurements of the factors of the environment; and the physiological responses of the plants in terms of transpiration, photosynthesis, and growth. From 1927 to 1929, this work was conducted in the oak-hickory forest fringing the Missouri River at Peru, in southeastern Nebraska.

The great amount of labor involved in the excavation of the root systems of trees has been the principal deterrent in such investigations. In the study of the roots of mature trees, European workers have accomplished more than Americans. In America, however, initial root habit of trees has been more extensively studied.

Nobbe experimented with the roots of conifers in Germany as early as 1875. He discovered striking differences in various species grown under similar conditions (cf. Jost, '07). During the 50 years following Nobbe's work, isolated investigations, especially in Germany and Russia, have laid the foundations for the studies of tree roots published since 1925. An excellent resumé of the work of European investigators is given by Büsgen and Münch ('29).

Toumey ('28, '29), as a result of his extensive experiments in Connecticut, concludes that initial root habit of American trees depends upon the species and in most cases is not essentially modified by external conditions. Pulling ('18), working in the far north, found that species vary in the degree of flexibility of the root habit which they exhibit under a change of environmental conditions. Haasis ('21), as a result of extensive studies in Arizona, found that soil type greatly modifies the root form of *Pinus ponderosa scopulorum*. Wahlenberg ('29), in Montana, investigated the possibility of modifying the root form of western yellow pine in seed beds by fertilizing the soil at different depths.

Studies of the development of *Fraxinus lanceolata*, *Acer negundo*, *A. saccharinum*, and *Gleditsia americana* were made in eastern Nebraska (Clements, Weaver, and Hanson, '29). These species were grown for a period of 3 years under various degrees of competition. The root system of each was

characteristic of the species, but greatly modified in depth and degree of branching by various degrees of competition with grasses.

Laitakari ('27), in his extensive studies in Finland, found that the roots of mature trees of *Pinus sylvestris* rarely exceeded a depth of 1.5 meters, and that the longest laterals seldom exceeded 17 meters. Gursky ('28) studied root systems of *Fraxinus excelsior*, *F. pennsylvanica*, and *Acer negundo* in the Caucasus. He concluded that even related species may differ in type and depth of root systems.

Selection of Stations

The forests of eastern Nebraska are an extension of the oak-hickory (*Quercus-Hicoria*) association northwestward along the Missouri River. Owing to the fact that the trees are mostly near the limit of their range, the grouping according to slope and consequent water relations is very clearly

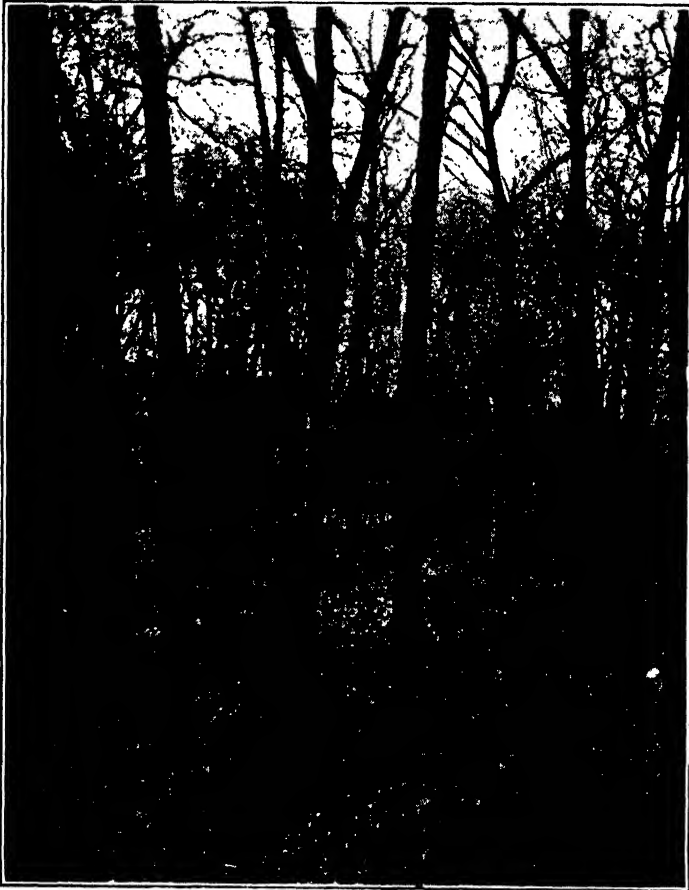


FIG. 1. General view of forest site of *Quercus macrocarpa* and *Q. velutina* at Peru, Nebraska, May 10, 1927, before the shrubs had developed their leaves.

defined (cf. Transeau, '05). On the flood plains and in wet ravines white elm (*Ulmus americana*), red elm (*U. fulva*), black walnut (*Juglans nigra*), and green ash (*Fraxinus lanceolata*) are characteristic species. The well drained, moist, and sheltered lower slopes are dominated by linden (*Tilia americana*), which intermingles with red oak (*Quercus rubra*) and then is replaced by it on the mid-slopes. The shellbark hickory (*Hicoria ovata*) is usually associated with the red oak, but sometimes occurs in nearly pure stands on slightly drier soils. A mixed forest of black and bur oak (*Quercus velutina* and *Q. macrocarpa*) occupies upper slopes, the latter alone dominating on the drier upland (Weaver, Hanson, and Aikman, '25; Aikman, '29).

The species selected for study were *Juglans nigra*, *Tilia americana*, *Quer-*



FIG. 2. Detail of forest floor at the linden (*Tilia americana*) station, on a cool, moist, north slope. Note the scarcity of shrubs and tall herbs, Sept. 10, 1927.

cus rubra, *Hicoria ovata*, and *Quercus macrocarpa*. They were grown in each of 3 sites. The first site selected was a steep, north-facing slope in a typical *Tilia* community; the second was a gentle southwest slope occupied by a community of *Quercus macrocarpa* and *Q. velutina*; and the third a cleared area now under cultivation on a gentle, south slope near the crest of the same hill (Figs. 1 and 2). This hilltop was partly covered by prairie grasses, although the place where the seedlings were grown was entirely free

of vegetation. These sites, which are all within one-fourth mile of each other, hereafter will be designated as the linden, oak, and prairie stations.

NATURAL VEGETATION

A survey of the vegetation was made at the 2 forest stations in order to interpret more accurately the growth of the seedlings in relation to their environment. All trees over 6 feet in height, shrubs over 3 feet tall, and lianas over 5 feet long and within a radius of 100 feet of each station were listed. This included an area of 0.72 acre. At the bur-oak station there were 29 bur oaks and 40 black oaks. These were the largest trees, a few 15 inches in diameter, and constituted the dominant forest element. Only 5 red oaks and 3 small lindens were found. There were 36 red elms, mostly very small, unthrifty trees, and in addition 5 small, white elms, 4 yellow oaks (*Quercus acuminata*) and 4 wild black cherry (*Prunus serotina*).

At the more mesic station, the dominant was linden, represented by 64 trees, a few of which were 16 inches in diameter. The characteristic under-story of *Ostrya virginiana* was composed of 163 trees. Red oak was represented by 14 trees, mostly on the upper part of the slope, and here occurred 9 each of bur and yellow oak and bitternut hickory (*Hicoria minima*). The elms were well represented with 85 small trees of *Ulmus americana* and 31 of *U. fulva*. *Quercus velutina* (3), *Morus rubra* (34), *Fraxinus americana* (41), *Cercis canadensis* (15), and one or two each of *Prunus serotina*, *Acer negundo*, and *Populus deltoides* completed the list. The relative density of the trees is shown by the fact that at the oak station each of the 126 individuals had an average area of about 250 square feet. But at the linden station, where there were 481 trees, this was reduced to 65 square feet per individual.

Shrubs were far more abundant in the better lighted oak forest where they were represented by 9 species. Here there were over 1,000 stems. The 4 most important species were *Cornus asperifolia*, *Xanthoxylum americanum*, *Rhus glabra*, and *Rubus strigosus*. These were also found at the linden station together with *Corylus americana* and *Euonymus atropurpureus*, where, however, the total number of all species was only 65, and they were half-starved specimens. A somewhat similar relation held for the lianas—*Celastrus scandens*, *Rhus toxicodendron*, *Vitis vulpina*, *Parthenocissus quinquefolia*, and *Smilax hispida*. The ratio was 3 to 1, lianas also being more abundant in the oak forest. The last species was not found at the linden station. Thus the rather open, oak woodland with an abundant undergrowth contrasted sharply with the almost bare forest floor beneath the dense shade of the lindens.

Methods of Procedure

Seeds of *Juglans nigra*, *Quercus rubra*, *Hicoria ovata*, and *Q. macrocarpa* were planted in quantity at each station. Seed was collected locally and

stratified during the winter in alternate layers of soil and sand. Since experience had shown that *Tilia americana* failed to give satisfactory germination the first year, native seedlings of this species were secured from the linden station and transplanted at each station, without disturbing the root systems. This was done soon after the cotyledons had unfolded. The seedlings at the linden station were not transplanted. The places where the seeds germinated naturally were permanently located by means of small stakes. Special care was taken to keep conditions at the 3 stations as nearly natural as possible.

Preliminary experiments had revealed the fact that rodents, especially field mice and timber squirrels, were very destructive to seeds and seedlings. Their ravages were partly overcome by very late fall planting, just preceding the freezing of the soil, and by protecting the plants set out in spring with cylinders of woven wire. The wire was of one-half inch mesh and the cylinders were 15 feet long and 12 inches in circumference. They were closed at the ends and placed horizontally in trenches 7 inches deep. The seeds were then planted along the center of the cylinders as the trenches were filled with soil. Damage to the rows of seedlings was further prevented by arching over them long strips of woven wire firmly fastened at the surface of the soil.

The form, habit, and extent of the roots of 1-, 2-, and 3-year-old seedlings were determined by excavation. The number of leaves, their total photosynthetic area, and the length and diameter of stems were recorded at 3 different periods during the first growing season, and once each season thereafter.

Seedlings of bur oak, red oak, shellbark hickory, and linden were grown in phytometer cans for the determination of transpiration. The rapidity of food manufacture was also ascertained.

Environmental factors were quantitatively determined for the entire period of the growing season. These data include the aerial factors of humidity, temperature, evaporation, wind, light, and precipitation, and also mechanical analysis, water content, pH, and temperature of the soil.

The Environment

SOIL

The soil at all 3 stations is very similar, consisting of a fine silt loam known as loess (Table I).

The texture of the soil in the prairie and oak forest is almost identical; that of the linden station contains 8 to 15 per cent more silt and a proportionately smaller amount of sand (Table I). This increases its water holding capacity, but at the same time decreases aeration. The former varies from about 55 per cent at the prairie station (Hilgard method) to approximately 70 per cent in the linden forest. At no time was there deficient aeration at any of the stations.

TABLE I. *Mechanical analyses and hygroscopic coefficients of soils at the 3 stations*

Station and depth	Fine gravel	Coarse sand	Medium sand	Fine sand	Very fine sand	Silt	Clay	Hygro. coef.	pH
Prairie, 0-6 in.....	.1	.2	.3	2.4	29.2	41.7	26.1	8.5	7.6
Prairie, 6-12 in.....	.1	.1	.1	1.0	33.1	37.9	28.1	8.3	7.6
Prairie, 12-24 in.....	.1	.1	.0	1.1	33.2	39.9	25.8	8.6	7.6
Oak forest, 0-6 in.....	.0	.0	.3	.6	30.7	42.3	26.1	9.4	6.5
Oak forest, 6-12 in.....	.0	.0	.0	.3	36.0	35.1	28.5	9.0	6.3
Oak forest, 12-24 in.....	.0	.0	.0	.2	36.5	36.3	26.9	9.4	6.1
Linden forest, 0-6 in.....	.1	.2	.4	1.8	21.3	50.8	25.4	9.9	6.2
Linden forest, 6-12 in.....	.1	.2	.2	1.3	20.9	50.9	26.3	9.3	6.8
Linden forest, 12-24 in.....	.1	.2	.2	1.5	29.7	44.3	24.1	8.8	6.6

There is a slight increase in the hygroscopic coefficient of the surface 6-inch layer from 8.5 to 9.9 proceeding from prairie through oak woodland to the linden forest (Table I) (cf. Aikman, '29). It seems probable that this is due largely to differences in the amount of organic matter. A similar relation holds for the second 6-inches of soil but not for the second foot.

Soils of the forest are slightly acid (pH 6.8 to 6.2) and those of the prairie slightly alkaline (pH 7.6), but the deviation from neutrality is too small to be of much importance in the growth of plants.

WATER CONTENT

Soil samples were taken in duplicate at each station twice each week from June 1 to October 1, 1927. The usual technique was followed in securing

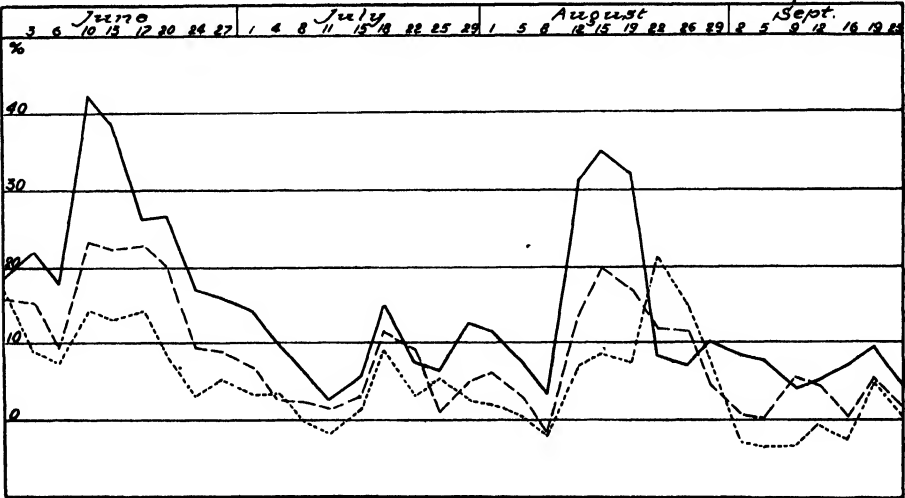


FIG. 3. Water content in excess of the hygroscopic coefficient in the surface 6-inch layer of soil at the 3 stations during 1927. Here, as in the graphs following, the short, broken lines indicate conditions at the prairie station; the long, broken lines in the oak forest; and the heavy line in the linden forest.

the samples and drying them in the electric oven (Weaver and Clements, '29). The depth classes were 0-6 in., 6-12 in., and 12-24 in. Percentage of moisture was computed on the basis of dry weight, and the average percentage of the 2 samples was recorded.

It is clearly apparent that the water content was greatest at the linden station, intermediate in the oak forest, and least in the prairie (Fig. 3). The hygroscopic coefficient was not reached at the linden station at any time during the growing season; at the oak station it was reached only for a brief

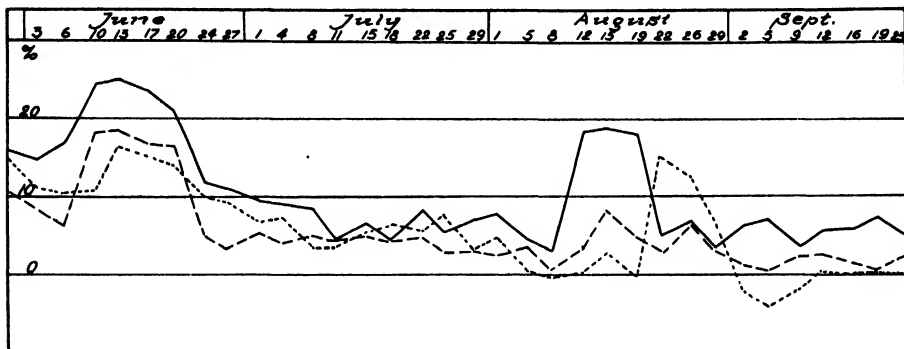


FIG. 4. Water content in excess of the hygroscopic coefficient at the 6 to 12 inch level at the several stations.

period early in August; but at the prairie station a deficit of water occurred during the second week of July, the first week of August, and throughout the first half of September. By the second week in July, however, the tap-roots of all the trees except the linden were well beyond the depth affected by drought. The lindens were aided by watering at the prairie station.

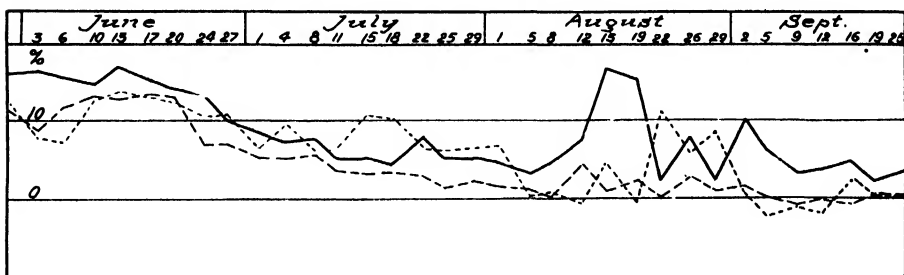


FIG. 5. Water content in excess of the hygroscopic coefficient at the 12 to 24 inch level.

The water content at a depth of 6-12 inches was also highest at the linden station, although the total amounts were somewhat lower (Fig. 4). In the oak forest also, the second 6-inches of soil were drier than the surface 6-inches, but at the prairie station the reverse was true. Obviously the shade of the forest tends to prevent the drying of the surface soil. The hygroscopic coefficient in this deeper soil layer was not reached at any of the

stations until the first week in August, and then at the prairie station only.

There was an increase in water content of the second foot at the prairie station and a decrease in the forest (Fig. 5). The differences in soil moisture at the 3 stations decrease with depth. Also the greater the soil depth the later in the season is the hygroscopic coefficient reached. In the second foot, moisture did not fall below the hygroscopic coefficient until the second week in August, and then in the prairie only, though it reached the hygroscopic coefficient at the oak station (Fig. 5). A water deficit again occurred in the prairie during most of September.

Because of increased rainfall, water content was higher at all 3 stations during the summer of 1928. In the 0 to 6-inch level water was available for growth at all times at both forest stations, but 3 periods of deficiency occurred in the prairie (Fig. 6). In the second 6-inch level there was always

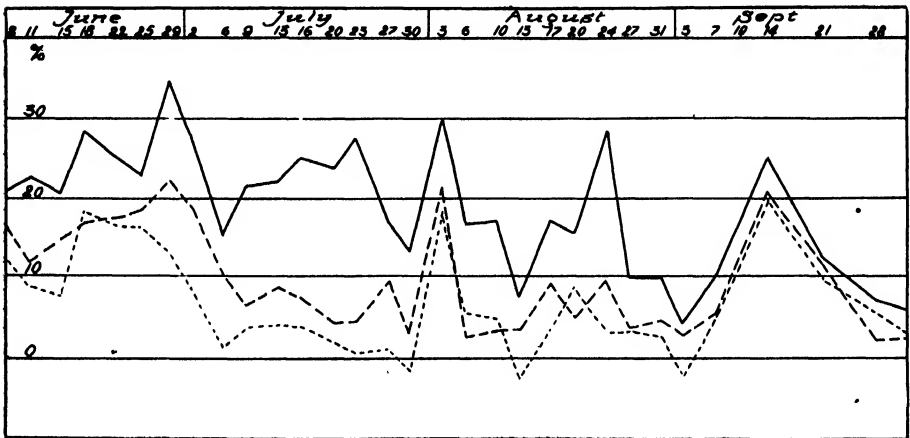


FIG. 6. Water content in excess of the hygroscopic coefficient in the surface 6-inch layer of soil at the 3 stations during 1928; compare with figure 3.

4 or 5 per cent of water available at the linden station, and usually 10 to 20. In the oak forest, water content was slightly below the hygroscopic coefficient for a brief period in the middle of August, otherwise 4 to 8 per cent was available. Smaller amounts were available in the prairie soil, and the hygroscopic coefficient was reached twice. Water was never non-available in the second foot of soil. The available water content was not high, however; even that at the linden station ranged between 5 and 22 per cent. The deeper soil, even of the prairie, was fairly well supplied with water to many feet in depth.

Excessive rains in 1929 made water available at all 3 stations and at all depths throughout the growing season.

RAINFALL

Rain gauges were placed at each station and read after each rainy period during the growing season of 1927. In this manner the amounts intercepted by the forest canopy were determined, although no account was taken of the amount of water that might have reached the ground by running down the tree trunks (Horton, '19). The mean annual rainfall at Peru, Nebraska, is 34 inches. The summer of 1927 was unusually dry, but the rain was well distributed throughout the growing season, 1.7, 2.2, 4.7, and 5.2 inches occurring during June, July, August, and September, respectively.

At the oak station 16.1 per cent of the rainfall was intercepted and 27.2 per cent by the denser canopy of the linden forest. Other factors such as decreased evaporation operate to balance this loss of moisture at the forest stations.

The growing season of 1928 was one of greater rainfall than the preceding and the showers were well distributed. The total rainfall for the growing season was 21.09 inches. Interception in the oak forest reduced the water reaching the gage to 18.7 inches. Interception was less in 1929 than in 1927, since during the very wet summer of 1929 the rains were torrential while those of 1927 consisted of lighter showers. The total rainfall at the several stations during the growing season of 1929 was 27.1, 25.4, and 24.0 inches, respectively.

EVAPORATION

The rate of evaporation was determined at each station for the period of June 1 to October 1, 1927. For this purpose, Livingston's standardized, white, cylindrical cups were used. The apparatus was run in duplicate, each cup being fitted with a non-absorbing device. Readings were made once each week, and the losses reduced to those of the standard cups.

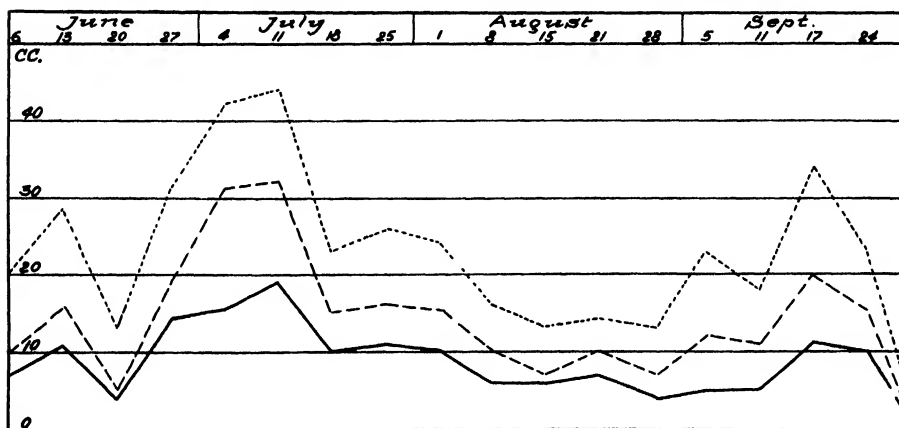


FIG. 7: Average daily evaporation at the several stations during 1927.
(Legend as in figure 3.)

Evaporation for the entire season at the oak station was only 59 per cent of that at the prairie, where the average daily losses ranged from 14 to 44 cc., while at the linden station it was reduced to 23 per cent of that at the prairie station, and to 40 per cent of that at the oak station (Fig. 7). The relatively xeric aerial conditions on the open prairie are, without doubt, highly detrimental to the establishment of trees, while mesic conditions within the forest are favorable. Upland trees, such as bur oak, have become adapted to dry sites by extending their taproots deeply (usually about 9 inches) before unfolding their leaves (Fig. 8). Roots of shellbark hickory reach a length of

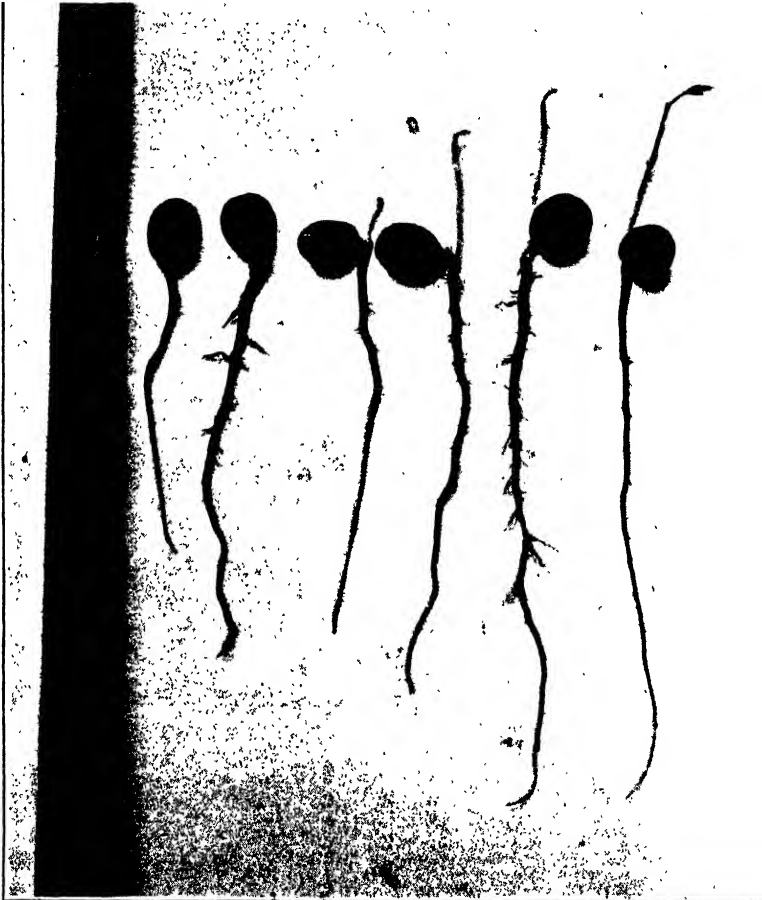


FIG. 8. Stages in the germination of *Quercus macrocarpa*, showing the relative development of roots and tops.

8 inches and those of red oak 7 before the leaves begin to unfold. Those of the linden are 2 inches or less. Apparently there is a direct relation between the dryness of the site and the length attained by the roots before the unfolding of the leaves.

The sequence of average daily evaporation rates in 1928 was similar to that of the preceding season. It was highest in the prairie (14 to 28 cc.), intermediate in the oak forest (8 to 18 cc.), and lowest at the linden station (4 to 6 cc.). In general, the losses were lower than in 1927 and no periods of stress occurred, as in July, 1927.

WIND

Anemometers of the standard Weather Bureau type were placed at a height of 12 inches, and in such places that they could not come in contact with the vegetation. They were read once a week at each station from June 1 to October 1, 1927.

The greatest average wind velocity, that on the prairie, did not exceed 4.5 miles per hour. There were days, however, when the average rate reached 11 to 12 miles per hour, and transpiration was greatly accelerated. In the oak forest, wind velocity was reduced to 29 per cent of that in the prairie, and to only 10 per cent at the linden station. Wind is a factor of considerable importance; a direct correlation between wind movement and evaporation was found.

In 1928, wind movement was slightly greater and fluctuated somewhat less than in the preceding summer. It varied in the prairie from an average daily velocity of 0.6 to 4.2 miles per hour. The cover of the oak forest reduced the velocity to about 0.4 to 1.5 miles; at the linden station it ranged between 0.36 and 0.45 mile per hour.

HUMIDITY AND AIR TEMPERATURE

Continuous records of humidity were obtained at the 3 stations from hygrothermographs appropriately sheltered and placed at a level with the seedlings. Average daily humidity at the prairie station was much lower than at the linden station, where the average day humidity seldom fell below 65 per cent and frequently exceeded 80 per cent (Fig. 9). No consistent

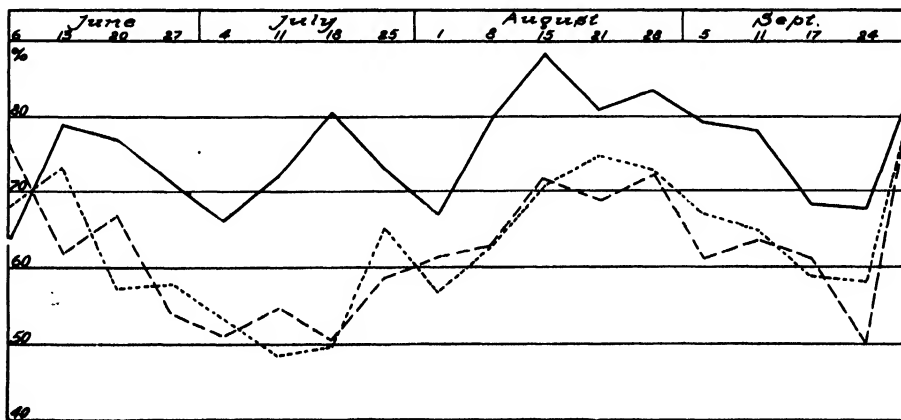


FIG. 9. Average day humidity at the 3 stations during 1927.

difference was found between the other 2 stations, probably because the prairie hilltop was entirely surrounded by forest and sufficient air movement occurred to keep the air moisture fairly well distributed. At both the prairie and oak stations the humidity often ranged from 10 to 15 per cent lower than in the linden forest, and differences during periods of stress were often much greater.

The lowest average temperatures, during the day, occurred at the linden station and the highest in the prairie (Fig. 10). After mid-summer the

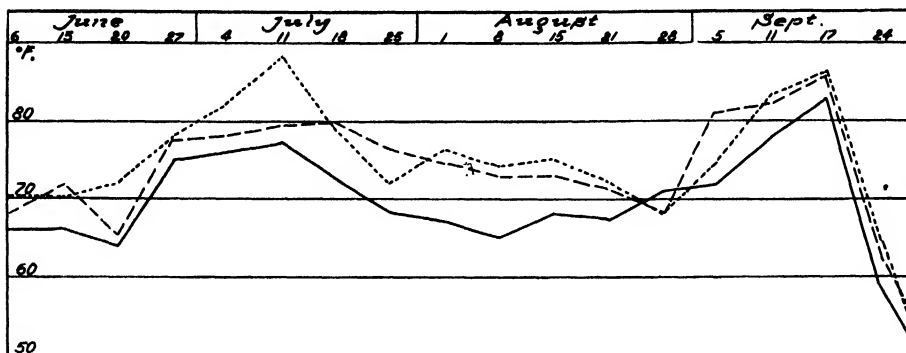


FIG. 10. Average day air temperatures at the 3 stations during 1927.

average temperature at the oak station often exceeded that of the prairie. Differences in average night temperatures were small, seldom exceeding 5° F.: although there was considerable irregularity, the tendency was toward the lowest at the prairie station, highest in the oak forest, and intermediate ones at the linden station. The average temperature for both day and night was lowest in the linden forest, with much intersecting of the graphs for the oak and prairie stations. Extreme differences at the several stations rarely exceeded 5° F. and were usually less.

The mean weekly humidity and temperature computed upon the daily maxima and minima, reveal the fact that extremes both of humidity and temperature were greatest in the prairie, least at the linden station, and intermediate in the oak forest. These higher temperatures at the prairie station, combined with greater wind velocities, were instrumental in maintaining a higher rate of evaporation and transpiration. Conversely, the lower temperatures and still air at the linden station reduced the rate of evaporation. Seedlings at the prairie station were growing under more severe aerial conditions than those in the dense linden forest, while those at the oak station were subjected to intermediate conditions.

During 1928, air temperatures were very similar in general to those recorded for 1927. The average daily maximum air temperatures of the prairie were always 1° to 9° F. higher than those of the oak forest, where, in turn, they were consistently 1° to 10° higher than at the linden station,

which ranged from 70° to 82°. No such differences were found for average daily minimum temperatures, first one station, and then another holding the highest or lowest place.

Owing to excess precipitation and much cloudy weather, humidities were somewhat higher in 1928 than in 1927. Day humidities in general were lowest on the prairie, slightly higher in the oak forest, and markedly so at the linden station. Average differences of 10 to 30 per cent regularly occurred between the two forest stations. In 1929, the higher humidity and greater degree of cloudiness during the experimental period accounted for the lower transpiration losses.

SOIL TEMPERATURE

Soil temperature readings were made twice each week between 3 and 4 P.M. by inserting thermometers in the holes made by the geotome in securing samples of the soil for water-content determinations.

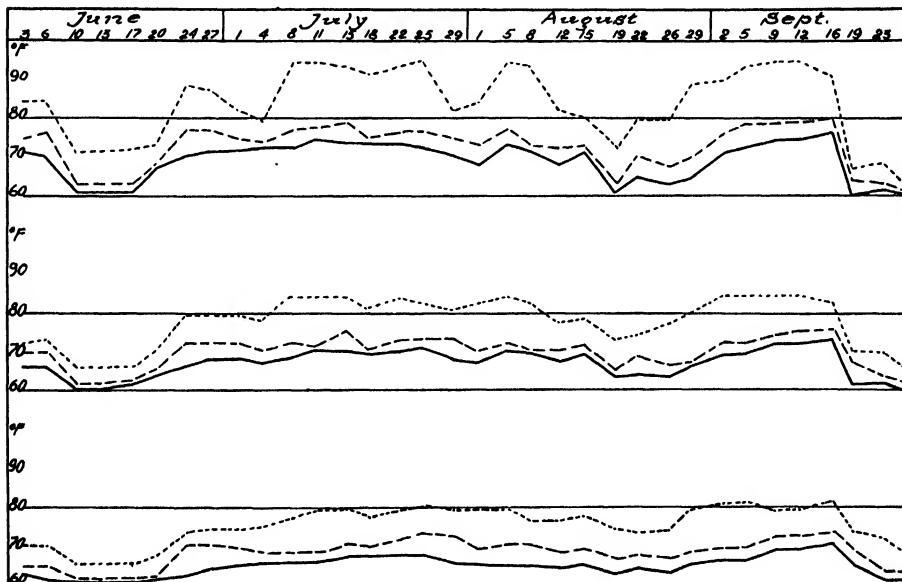


FIG. 11. Soil temperatures at the 3 stations during 1927: upper graphs, at a depth of 6 inches; middle, at 12 inches; and lower, at 24 inches.

Temperatures were consistently highest at all depths at the prairie station, intermediate in the oak woodland, and lowest in the linden forest (Fig. 11). At a depth of 6 inches, the prairie soil was usually 18° F. warmer than that of the linden forest. This difference decreased to 13° at the 12-inch level and 11° at 2 feet. Temperatures of 95° were not uncommon at the prairie station at the 6-inch level, and 82° at 12 inches in depth, but at the linden station a temperature of 65° or less was not infrequent at a depth of 12 inches. These differences in soil temperature are sufficient to affect pro-

foundly the rate of growth of roots (Cannon, '15; Toumey and Neethling, '24).

Soil temperatures are an important factor in the germination of seeds and establishment of seedlings. This is particularly true of the surface layer of soil, and it is here that the greatest daily fluctuations occur. Temperatures at the linden station are too low to promote as rapid germination and vigorous growth as at the other stations.

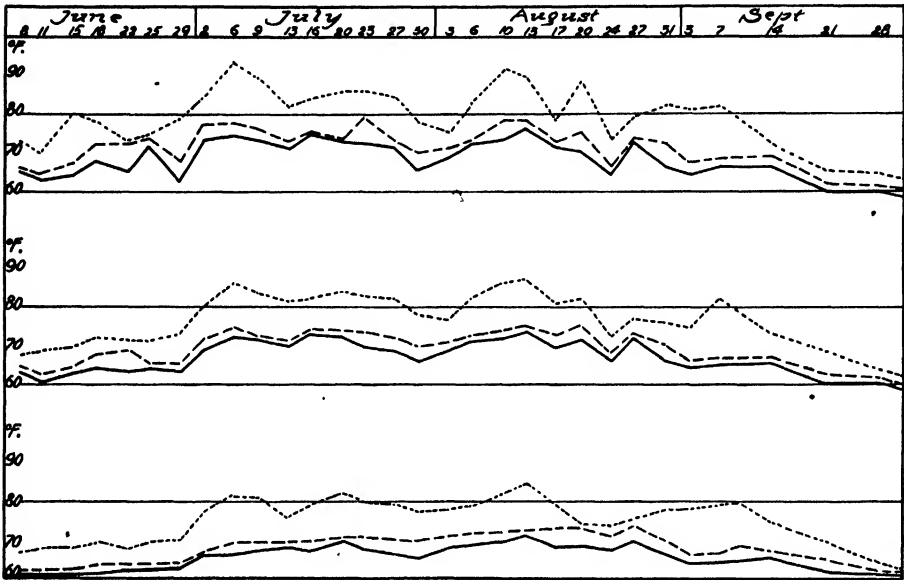


FIG. 12. Soil temperatures at the 3 stations during 1928: upper graphs, at a depth of 6 inches; middle, at 12 inches; and lower, at 24 inches.

Soil temperatures of 1928 (Fig. 12) were very similar to those of 1927 (cf. Fig. 11) except that the surface soil at the prairie station, owing to increased moisture content, averaged about 8° F. cooler. The higher temperatures at the prairie station accelerated the physical and chemical processes accompanying growth, as is plainly revealed in root behavior.

LIGHT

Measurements of the intensity of light during the summers of 1927 and 1928 were made by the use of Clements' photometer. Readings were taken only on clear days, twice each month, and at 2-hour intervals. In making the readings care was taken to move the photometer back and forth so as to get an average of the prevailing light intensity under the crowns of the trees at the height of the seedlings. The values in Table II are typical for both seasons.

Light at the oak station averaged 10.4 per cent for the season, but only

TABLE II. *Average light intensity at the forest stations during 1928, in per cent, on the basis of the prairie station as 100 per cent*

Station and date	6 A.M.	8 A.M.	10 A.M.	12 M.	2 P.M.	4 P.M.	6 P.M.
June 18							
Oak.....	5.1	6.8	6.9	5.9	4.4	5.7	5.8
Linden.....	1.1	1.7	1.7	2.8	1.0	3.8	1.3
July 2							
Oak.....	5.0	5.5	9.5	8.0	10.2	5.2	6.7
Linden.....	1.5	1.6	5.9	6.5	8.3	4.2	2.1
July 15							
Oak.....	5.3	5.5	20.8	20.0	20.0	11.6	10.0
Linden.....	1.8	2.0	6.6	10.0	4.6	4.3	2.5
July 30							
Oak.....	5.1	8.3	15.0	18.2	15.0	6.6	22.1
Linden.....	3.0	2.7	4.1	7.6	5.8	3.3	4.2
Aug. 13							
Oak.....	6.6	6.6	16.6	15.0	5.0	6.6	15.0
Linden.....	6.0	2.5	3.3	5.0	0.8	3.3	0.8
Aug. 28							
Oak.....	5.0	16.6	18.7	17.6	11.6	11.6	16.6
Linden.....	1.6	4.1	3.0	6.6	1.6	2.5	5.0
Sept. 11							
Oak.....	5.0	8.3	8.3	14.2	11.4	11.4	14.6
Linden.....	1.6	1.6	4.1	2.1	2.6	3.0	6.0
Average							
Oak.....	5.3	8.2	13.7	14.1	11.1	8.4	13.0
Linden.....	2.3	2.3	4.1	5.8	3.5	3.5	3.1

3.5 in the linden forest. That light is a primary factor in the establishment and growth of tree seedlings in forest habitats is shown by its effect upon photosynthesis (see Measurement of Photosynthesis, below).

Growth of Roots

During the four years of this study, 200 root systems were excavated by means of the trench method described by Weaver ('26), and typical ones drawn to show the exact position occupied by them in the soil. The total depth and spread of roots of one-year-old seedlings of all 5 species were greatest at the prairie station, least in the deep linden woods, and intermediate in the oak forest (Table III).

TABLE III. *Root growth of one-year-old seedlings, in inches*

Species	Prairie station		Oak station		Linden station	
	Total depth	Total spread	Total depth	Total spread	Total depth	Total spread
Bur oak.....	60	30	20	11	11	3
Hickory.....	28	7	14	4	11	2
Red oak.....	28	12	21	6	12	4.5
Linden.....	13 *	4.5 *	9	3.5	8	3
Walnut.....	54	48	24	22	23	21

* Watered.

Bur oak displayed its adaptation to uplands by sending a taproot to a depth of 5 feet at the prairie station. The strong development of the taproot was shown under all 3 types of environment, although it penetrated only

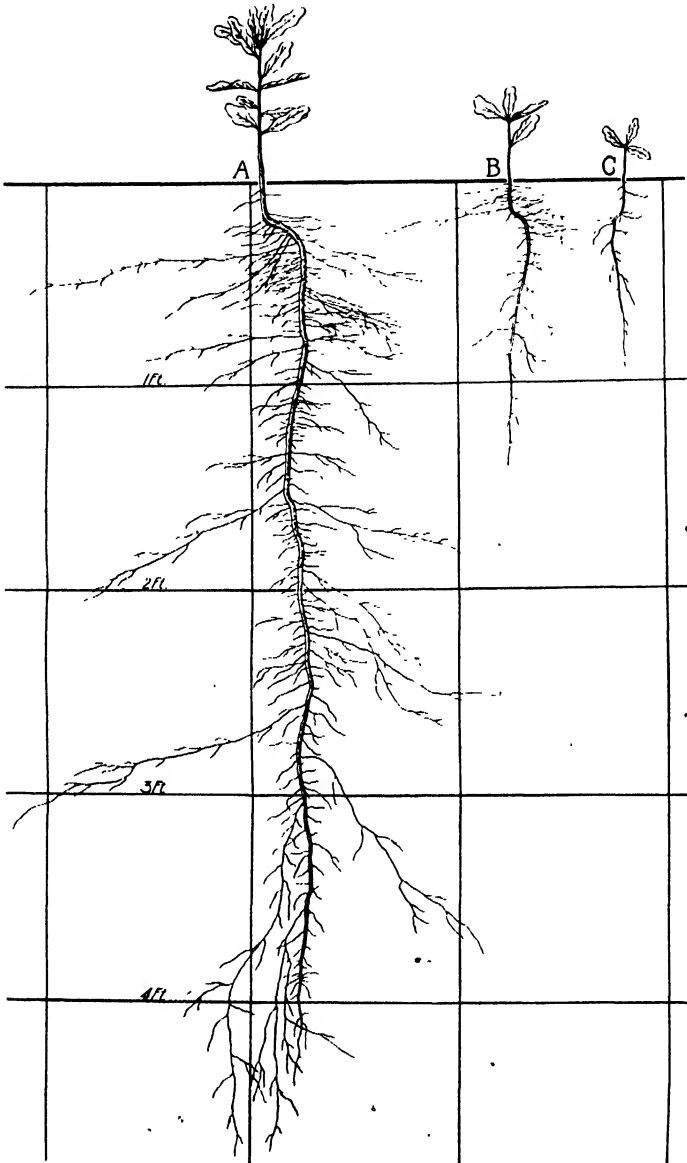


FIG. 13. Development of roots and tops of *Quercus macrocarpa*: **A**, on the prairie; **B**, in oak forest; and **C**, in linden forest; during their first season of growth.

one-third as deeply at the oak station and about one-sixth as deeply at the linden station as compared with the drier site on the hilltop (Fig. 13).

Shellbark hickory likewise showed its adaptation of roots to the more xeric conditions of the upper hillsides. It is of slower growth than bur oak, and its lateral spread of roots compared with its total depth is much less. At the linden station the growth of hickory and bur oak was approximately equal. The laterals of the hickory grow nearly at right angles to the taproot (Fig. 14).

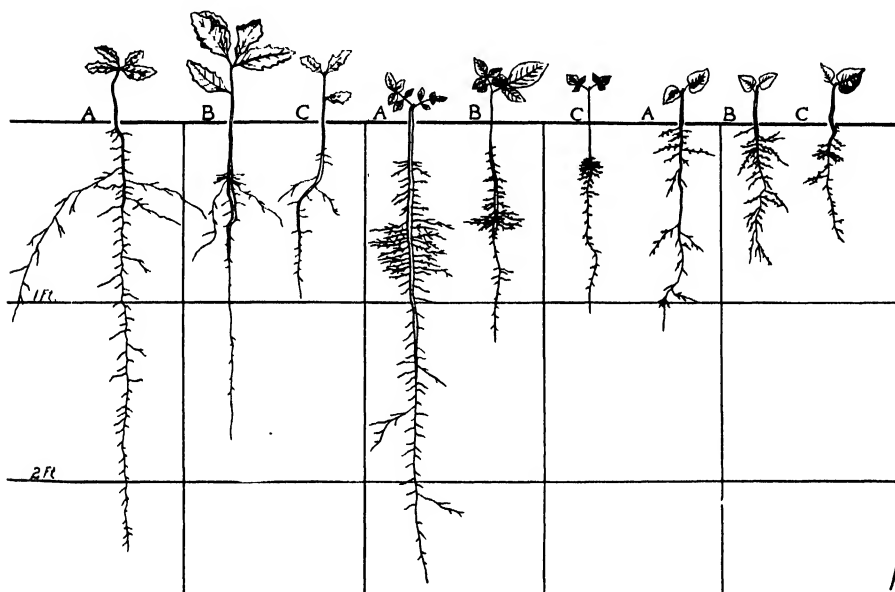


FIG. 14. Seedlings of *Quercus rubra* (left), *Hicoria ovata* (center), and *Tilia americana* (right), at the end of the first season of growth: A, from prairie; B, from oak forest; and C, from linden forest. The linden at the prairie station was watered.

Red oak displayed the taproot characteristic of most oaks (Toumey, '28, '29), but it tended also to produce one or more important laterals the first season. It was thus intermediate between bur oak and shellbark hickory on the one hand and linden on the other. As would be expected, red oak grew somewhat better at the linden station the first season than did the less shade-tolerant bur oak and hickory (Fig. 14).

Linden grew slowly in all 3 habitats. Numerous laterals were a prominent feature of the root system. Only a few seedlings survived to the end of the season under the relatively xeric conditions of the prairie station. Because of the shallow root system, it is doubtful if any would have survived had they not been repeatedly watered during the critically dry periods (Fig. 14).

Walnut extended its taproot nearly as deeply as bur oak at the prairie station, and its total spread almost equalled the depth. It grew only slightly more in the oak woods than at the linden station, but at the end of the season

appeared to be in much better condition in the oak forest where there was more light. Walnut developed at all 3 stations the most extensive root system of any of the 5 species (Fig. 15).

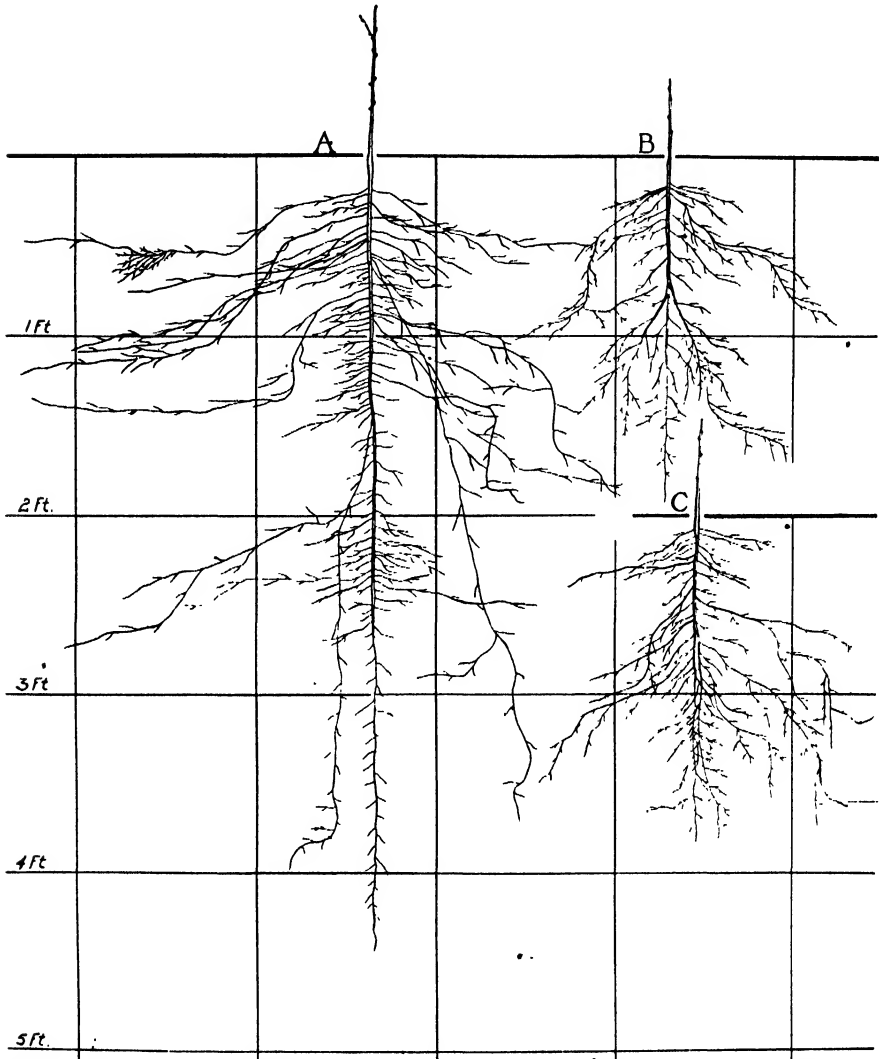


FIG. 15. Seedlings of *Juglans nigra* after one season of growth. The stations as before and to follow are: A, prairie; B, oak; and C, linden.

Two-year-old root systems were excavated in the fall of 1928. During the second year, growth in all of the species continued rapidly at the prairie station, only slowly at the oak station, and scarcely at all in the linden forest (Table IV). Each species maintained the same characteristic type of root that it possessed the first season. Those species which had made the best

growth the first season continued to outgrow the others during the second summer.

At the prairie station, bur oak extended its taproot 2 feet deeper than during the previous season, reaching the 7-foot level, and increasing its total spread about 8 inches (Fig. 16). Comparison of figures 13 and 16 shows

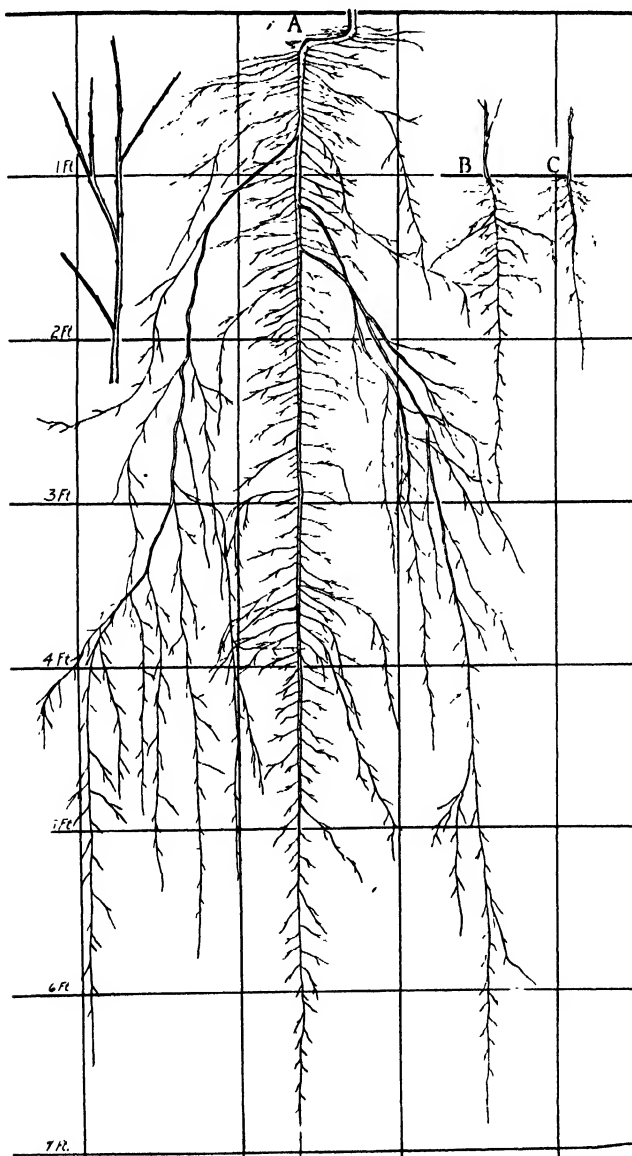


FIG. 16. Development of bur oak at the end of the second summer: **A**, in prairie; **B**, in oak forest; and **C**, in linden forest.

TABLE IV. *Growth of roots of three-year-old seedlings, in feet. Numbers in parentheses are for the preceding year*

Species	Prairie station		Oak station		Linden station	
	Total depth	Total spread	Total depth	Total spread	Total depth	Total spread
Bur oak	(7.0) 8.5	(3.2) 5.2	(2.0) 2.3	(0.8) 0.8	No plants survived	
Hickory	(3.0) 5.3	(2.0) 2.0	(1.4) 1.8	(0.4) 0.7	No plants survived	
Red oak	(3.6) 5.8	(2.2) 3.5	(1.7) 2.5	(0.5) 1.0	No plants survived	
Linden	(1.6) 5.3	(0.7) 6.5	(0.8) 1.3	(0.3) 1.1	(0.7) 0.7	(0.6) 0.7
Walnut	(6.6) 9.0 +	(5.5) 13.0 +	4.1	3.3	No plants survived	

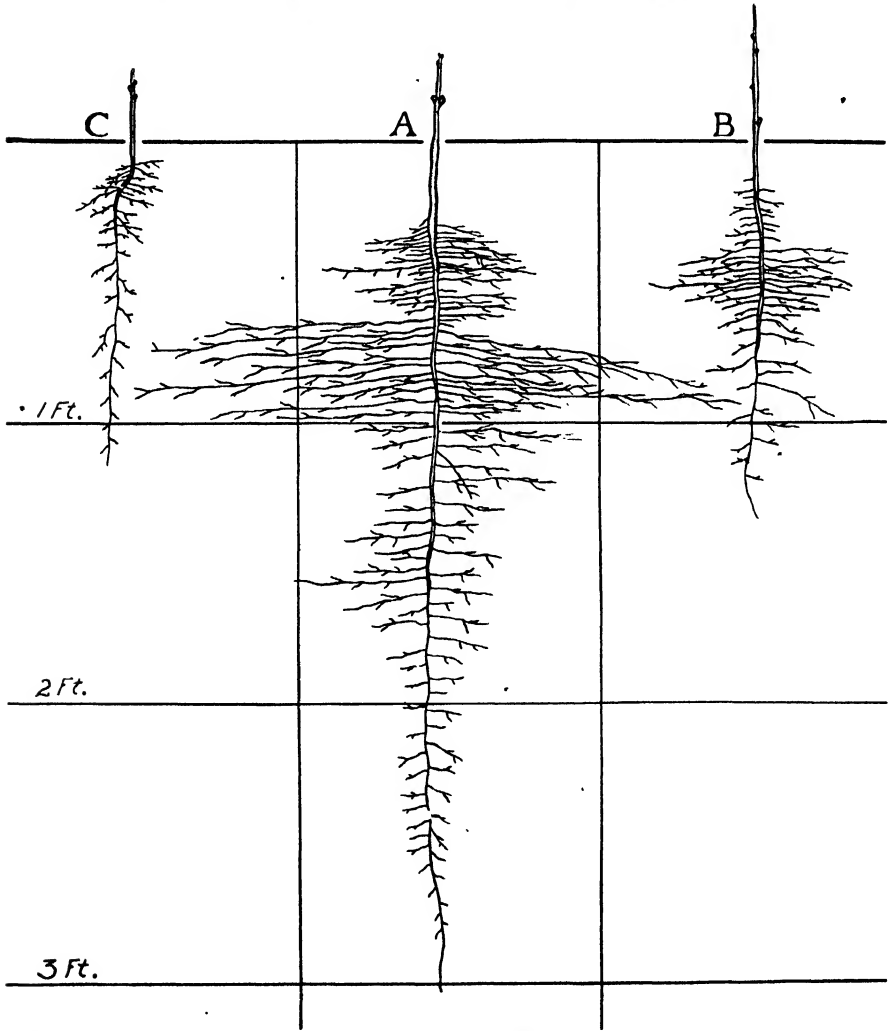


FIG. 17. Development of roots and shoots of shellbark hickory at the end of the second growing season. (Legend as in figure 16.)

that some of the strong lateral branches grew very rapidly. Growth was much poorer in the shaded habitats.

The hickory extended its taproot only an additional 8 inches but increased its spread to 24 inches. Only a few of its laterals, however, were so extensive (Fig. 17). Many strong laterals had been developed at the prairie station, and the same general type of branching characterized this species at

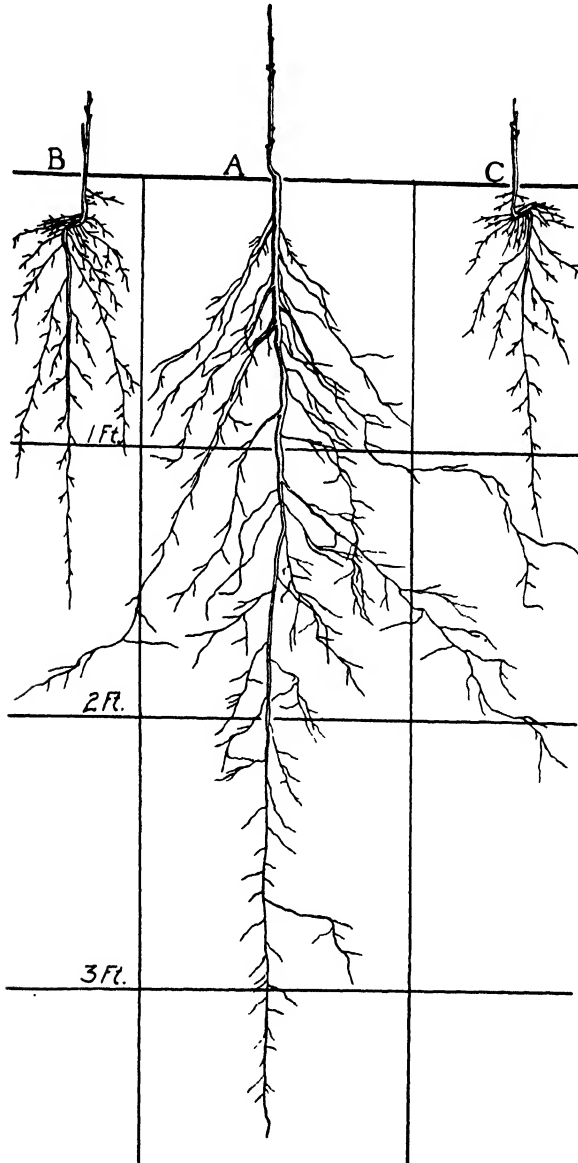


FIG. 18. Red-oak seedlings in the fall of the second year of growth.

the other stations, although more roots occurred nearer the surface of the soil than in the prairie. The almost horizontal spread of branches and the lack of development of any distinctly major laterals as compared with the bur oak is distinctive of the species.

Red oak grew downward an additional 15 inches and its total spread was 6.5 inches greater than at the end of the first year of growth (Fig. 18). Long, widely spreading laterals were pronounced.

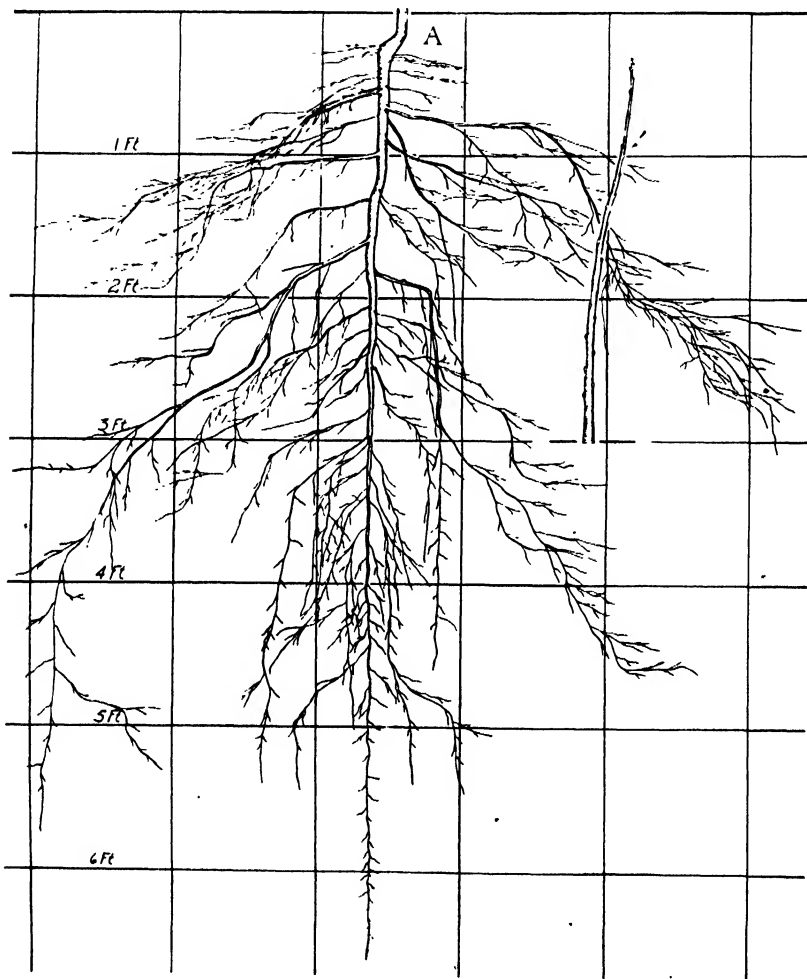


FIG. 19. Root and shoot of 2-year-old walnut seedling grown at the prairie station.

Walnut grew an additional 2 feet in length and increased its total spread 1.5 feet (Fig. 19). The development of many laterals became very apparent the second season.

The lindens, which had survived the first summer as a result of watering,

made a relatively poor growth (Fig. 20). Even in the prairie, where they did the best, the roots did not exceed 19 inches in depth and the spread was only about 8 inches.

Three-year-old plants were excavated in September, 1929. All of the species continued to make an excellent growth at the prairie station where

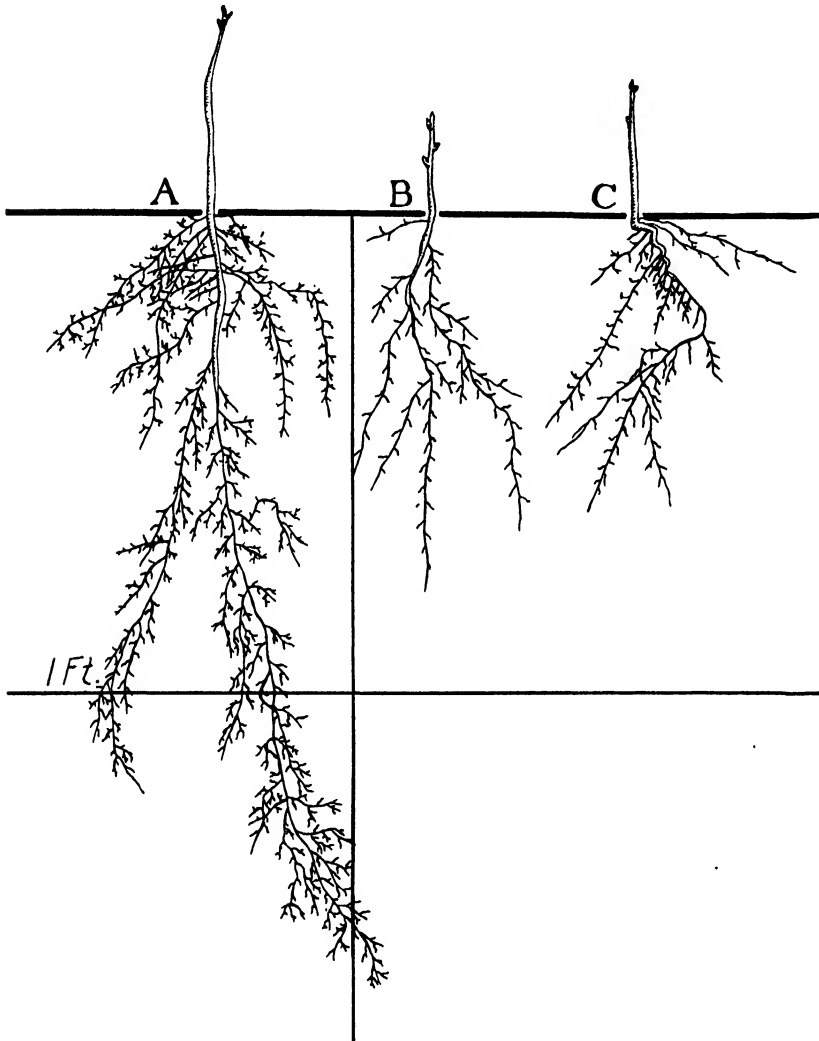


FIG. 20. Development of linden at the end of the second summer.

they were subjected to full sunshine (Table IV). Growth in the oak forest was poor, except in the case of walnut, while at the linden station *Tilia* alone survived. The poor conditions for growth at this station are shown by the fact that among 100 seedlings of linden growing naturally, only 61 survived

the first summer, and of these 19 winterkilled. Of the 42 remaining, 28 were alive at the end of the third year, although shallowly rooted under the moist duff.

The bur oak enlarged its soil area in the prairie by penetrating 1.5 feet deeper and extending its laterals 2 feet wider (Fig. 21). This rapid growth

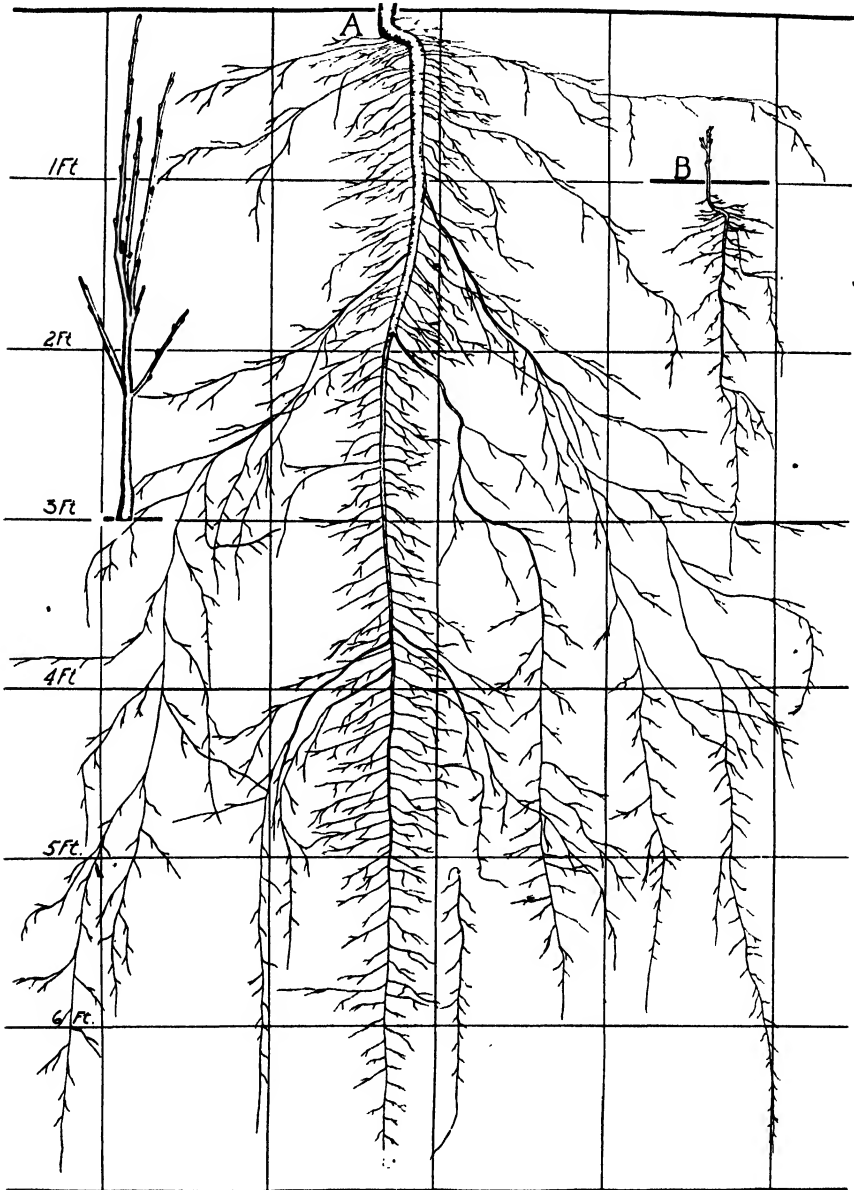


FIG. 21. Roots and tops of bur oak after 3 years of growth: A, in the prairie; and B, in the oak forest. None survived in the shade of the linden.

of its extensive taproot system explains its ability to thrive on upper slopes and exposed hilltops in soil so dry that all other native trees fail. In the oak forest its growth was slow.

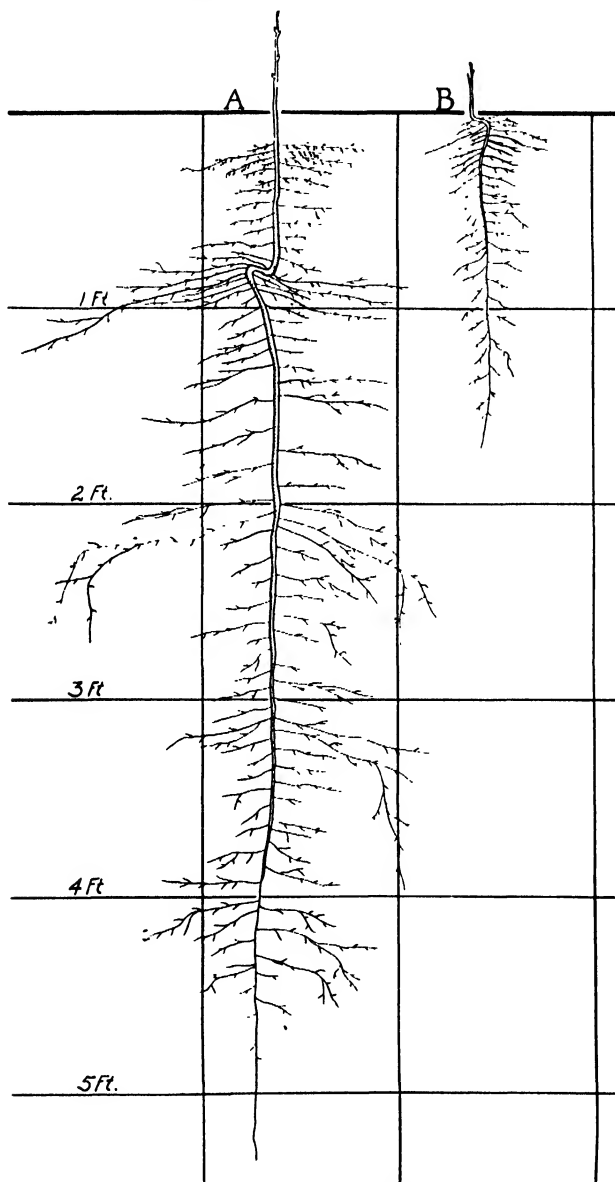


FIG. 22. Three-year-old seedlings of shellbark hickory in prairie and oak forest.

The strong taproot of the hickory was extended 2.3 feet deeper into the prairie soil, but the horizontal laterals did not spread farther than during the preceding year (Fig. 22). Comparing the extensive root system with the

relatively small top, it can readily be seen why hickory does well also upon uplands, if the air is not too dry.

The red oak made a really wonderful growth in the prairie, striking deeply and branching widely (Fig. 23). The root system was much better developed than that of the slower growing hickory but probably less so in relation

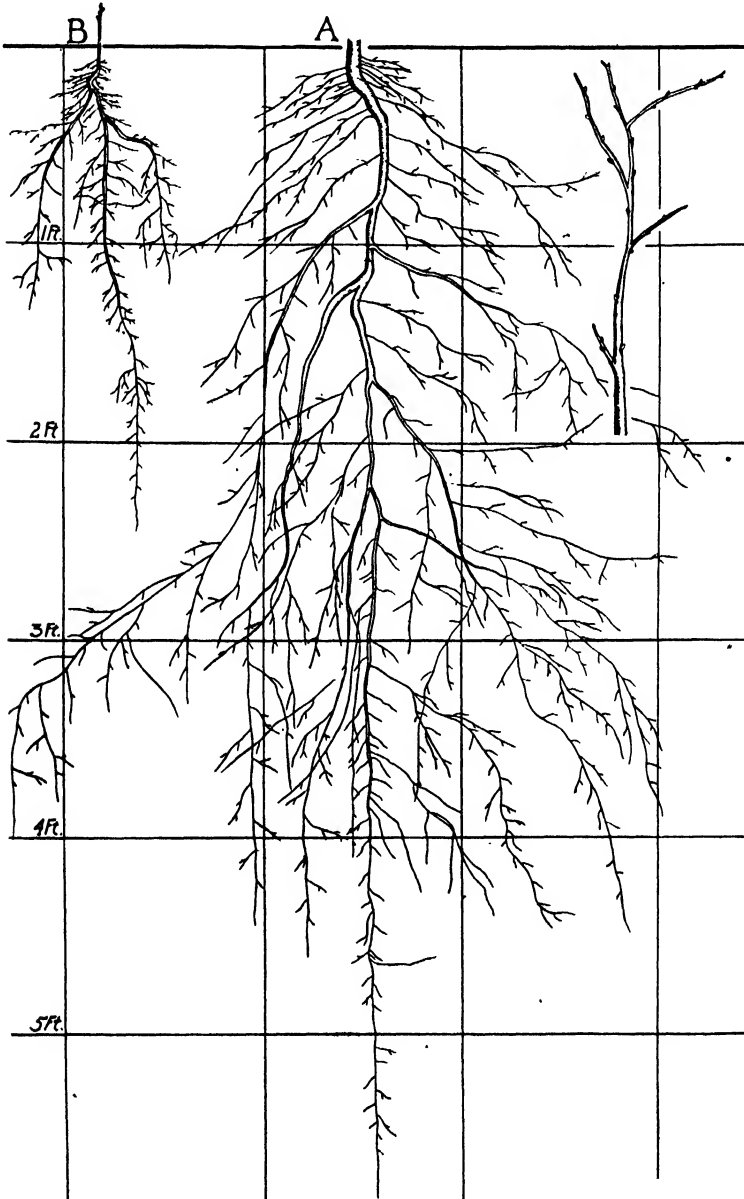


FIG. 23. Three-year-old seedlings of red oak grown in prairie and oak forest.

to tops. The taproots were exceeded in depth 2.7 feet and in lateral spread 1.7 feet by those of the bur oak. Growth was slow in the oak forest.

Even the very shade-tolerant linden did poorly under the parent trees, but much better in the oak forest. Once established in the fully lighted prairie, although suffering high mortality even when aided by watering, it made a remarkable growth. However, the bulk of the absorbing system was in the first 2 feet of soil, the relatively shallow root persisting even under conditions of impending drought (Fig. 24).

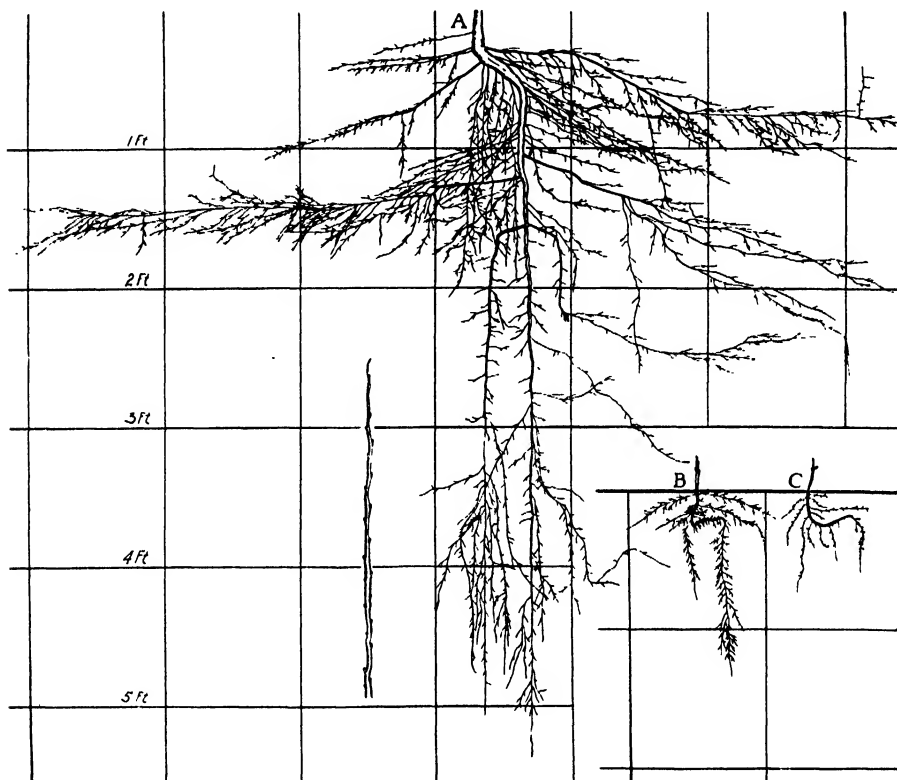


FIG. 24. Linden seedlings 3 years old. The impress of the habitat is clearly shown in the development of both roots and tops. This species alone survived in the linden forest.

The walnut, ordinarily at home along flood plains in this marginal forest, exceeded all the others in rate of growth in the prairie. The root system was not excavated in its entirety, but it was traced to a depth of 9 feet without reaching its end. Laterals were followed to a distance of more than 7 feet on all sides of the plant. The strong laterals, which probably spread more widely and penetrate less deeply in poorly aerated, flood-plain soil, admirably fit it for its usual habitat. The plasticity of its roots, which is greater than

that of many other species, together with its rapid rate of growth, enable it to enjoy a wider range of habitats when competition is not too severe.

TABLE V. *Growth of above-ground parts of first year tree seedlings*

Species	Stem diameter, mm.			Height, in.			No. of leaves			Area, sq. in.		
	July 15	Sept. 1	Oct. 15	July 15	Sept. 1	Oct. 15	July 15	Sept. 1	Oct. 15	July 15	Sept. 1	Oct. 15
Bur oak.....	4.0	4.4	4.4	4.1	8.0	8.0	7	15	18	25.4	34.8	32.1
Hickory.....	2.0	2.9	3.1	1.6	1.6	1.7	3	3	3	8.5	9.7	10.3
Red oak.....	3.2	4.5	4.6	2.0	4.1	4.0	7	12	14	29.1	36.2	35.6
Linden.....	1.6	2.9	2.9	1.5	2.1	2.5	3	3	F*	2.1	2.9	F
Walnut.....	4.2	6.2	9.5	6.0	9.1	10.0	10	12	F	151.8	198.1	F

Oak station

Bur oak.....	1.4	1.9	1.9	3.0	3.1	3.0	4	4	4	25.3	26.1	25.0
Hickory.....	1.6	2.0	1.9	1.8	2.0	2.2	3	3	3	4.2	8.9	7.3
Red oak.....	1.9	2.7	2.6	3.5	4.0	3.2	5	6	6	25.1	25.8	23.7
Linden.....	1.2	1.7	1.3	1.6	1.7	1.8	2	2	1	2.9	3.1	F
Walnut.....	1.9	3.5	2.9	2.5	5.1	5.3	5	F	F	112.7	F	F

Linden station

Bur oak.....	1.6	1.6	1.6	1.8	2.0	3.5	4	4	4	20.9	12.1	14.3
Hickory.....	1.5	2.3	1.9	2.2	2.5	2.6	2	2	2	6.5	6.3	6.0
Red oak.....	2.3	2.3	1.9	3.5	4.2	4.2	5	5	5	16.4	11.0	12.4
Linden.....	1.5	2.3	1.8	2.2	2.2	2.1	1	1	1	2.0	1.6	F
Walnut.....	2.8	2.6	2.5	6.0	6.1	6.0	5	F	F	41.9	F	F

* F signifies that the leaves had fallen.

Growth of Shoots

Data on the growth of shoots were obtained by measuring the diameters of the stems at the soil surface, by determining the height of stems to the tip of the terminal bud, by counting the number of leaves, and by measuring the total leaf areas. The last was found by making blue prints of the leaves and using the planimeter. These data are recorded in Table V, which gives a median of 13 trees of each species from typical plants at each station during the first growing season. These were measured at 3 different times and in the order in which they occurred in the row.

The above-ground parts of the seedlings are much less extensive than the root systems (Table V). In general, growth is greatest at the prairie station, least in the dense shade at the linden forest, and intermediate in the more open oak woods. Apparent inconsistencies, such as the decrease in leaf area of the bur oak from 21 inches on July 15, to 12.1 inches on September 1, are due to the depredations of insects, especially caterpillars. Decreases in diameter of stem and height of certain species at the linden and oak stations,

TABLE VI. *Growth of above-ground parts of two-year-old tree seedlings*

Species	Prairie station				Bur Oak station				Linden station			
	Number leaves	Area leaves, sq. in.	Diam. stem, mm.	Height, in.	Number leaves	Area leaves, sq. in.	Diam. stem, mm.	Height, in.	Number leaves	Area leaves, sq. in.	Diam. stem, mm.	Height, in.
Bur oak.....	69	443.0	12.7	22.5	2	7.6	2.1	3.9				
Hickory.....	4	12.0	4.1	3.0	3	13.1	2.5	2.6				
Red oak.....	38	210.8	6.9	11.0	6	16.1	2.7	3.4				
Linden.....	8	26.8	6.1	7.0	2	2.9	2.4	2.12	2	1.95	2.1	3.75
Walnut.....	*	*	18.2	35.5	8	72.8	3.6	7.0				

* Leaves so numerous that counting was impracticable.

appear to be due to actual shrinkage. Such seedlings rarely showed any signs of life the following spring. In the case of linden seedlings at the linden station, the decrease in diameter may be due in part to the difficulty of taking all 3 measurements at the same point, since the seedlings were growing in the natural duff of the forest floor. Slight increases in stem diameter and height at the prairie station from September 1 to October 15 indicate that growth may continue, under favorable conditions, after September 1.

Walnut made the greatest growth above ground of any of the species. Next in order were bur oak, red oak, hickory, and linden. Thus the greater the total extent of root system the greater also was the extent of the above-ground parts (Weaver and Himmel, '29; Crist and Stout, '29).

The tops were measured again on September 1 of the second summer. Several species were represented at the linden station only by remnants of the original stand, and at the prairie station the leaves of the walnut were, so numerous as to make measuring inexpedient. Since some of the seedlings measured the preceding year had died, especially at the forest stations, these measurements were secured from survivors previously measured and from other typical seedlings (Table VI).

The above-ground parts at the end of the second season were still much less extensive than the root systems. In general, growth was again greatest at the prairie station, least in the dense shade of the linden forest, and intermediate in the more open oak woods. Walnut had reached a height of 3 feet and a diameter of 18 mm. at the prairie station. It had surpassed all the other species in both the prairie and oak forest but, like the bur oak, hickory, and red oak, only a few starved specimens survived to the end of the second summer in the dense shade of the linden forest. Bur oak ranked next to the walnut in its rate of growth at the prairie station, but at the oak station, both of the more shade enduring species, hickory and red oak, excelled it in rate of growth. Data on the growth of linden at the prairie station are of really little significance, since the seedlings were enabled to survive the first season only because they were repeatedly watered during periods of drought.

The tops were again measured on September 1, 1929, in the third season (Table VII).

At the prairie station, walnut again made the greatest growth. Bur oak and red oak had both grown so much that their leaves were not counted. In hickory, the height of only 5 inches was in striking contrast with its extensive root system. The figures for linden at the prairie station are significant only in so far as they show the growth possible when this species has become well established.

Walnut still led in rate of growth of above-ground parts at the oak station. Red oak, bur oak, hickory, and linden followed in succession, although none of the last 4 species had greatly exceeded the growth attained during their second summer.

TABLE VII. *Growth of above-ground parts of three-year-old, tree seedlings*

Species	Prairie station			Oak station			Linden station		
	Number leaves	Diam. stem, mm.	Height, in.	Number leaves	Diam. stem, mm.	Height, in.	Number leaves	Diam. stem, mm.	Height, in.
Bur oak	*	21.1	36	4	2.5	3.6	None survived		
Hickory	6	5.9	5	3	2.4	2.6	None survived		
Red oak	*	12.8	23	6	3.2	3.5	None survived		
Linden	18	10.3	21	3	2.6	2.1	2	2.5	2.7
Walnut	*	36.4	68	9	5.3	15.9	None survived		

* Leaves so numerous that counting was impracticable.

Linden was the only species that survived the third summer under the dense shade of the linden forest, and its rate of growth was very slow.

Physiological Data

MEASUREMENT OF TRANSPIRATION

Transpiration of the several species in the 3 kinds of environment was determined by the use of phytometers. These consisted of seedling trees grown in containers 5.5 inches in diameter and 12 inches deep. Each container was provided with a small opening at one side near the base which permitted drainage; the top consisted of a sloping metal roof except for a circular opening, 2 inches in diameter, in the center. The seeds were germinated in the greenhouse in the containers, in soil taken from the stations. Linden was an exception, since the seedlings were transplanted. The phytometers were removed to the several stations upon the appearance of the shoots above ground. To insure natural conditions under the several environments, the containers were buried in the soil to within an inch of their tops. Water was added when necessary to keep the soil well moistened.

When the seedlings had reached a suitable size for the experiments, the phytometers were removed from the soil, the soil within them was brought to the original water content, and the openings for drainage were closed. A large cork was carefully fitted over the soil around the plants, and water-proofed. This effectively sealed the containers. After weighing, they were replaced in the soil for 10 days, when they were again weighed. Leaf prints were made on blue-print paper at the beginning and end of the period. These leaf prints were measured by means of a planimeter, and the 2 measurements were averaged to secure the photosynthetic area. The losses were calculated in grams per square centimeter for the 10-day periods. Two experiments were conducted in 1928 and two in 1929. At least 36 phytometers of each species were used.

TABLE VIII. *Average water loss in grams per square centimeter of leaf area at the three stations during 1928 and 1929*

Station and species	July 5-15, 1928	July 15-25, 1928	June 28-July 8, 1929	July 8-18, 1929	Average
Prairie station					
Bur oak	60.0	63.9	20.6	18.7	40.8
Hickory	55.5	58.1	21.3	20.6	38.8
Red oak	32.3	34.8	13.6	11.6	23.0
Linden	20.0	20.6	13.6	11.0	16.3
Average					29.7
Oak station					
Bur oak	29.0	31.6	17.4	11.0	22.2
Hickory	29.0	29.7	14.8	11.6	21.3
Red oak	14.8	18.7	11.6	10.3	13.8
Linden	18.1	18.1	9.7	9.7	13.9
Average					17.8
Linden station					
Bur oak	8.4	9.7	16.1	11.6	11.4
Hickory	7.1	11.6	12.9	11.0	10.6
Red oak	4.5	7.8	11.6	9.7	8.4
Linden	5.8	7.1	9.7	8.4	7.7
Average					9.5

With few exceptions, transpiration at the prairie station decreased as the mesophytism of the species increased (Table VIII). In some cases the bur oak transpired at 3 times the rate of the linden. A similar relationship held at the oak station, where the bur oak and hickory often transpired nearly twice as much as the red oak and linden. The trend was the same at the linden station, but here water losses were much smaller and the differences not so noticeable.

At the oak station, transpiration was nearly twice that at the linden station, and at the prairie station it was more than 3 times as great. At all 3 stations the upland species transpired much more than linden and red oak which characterize the lower slopes. The lower rates of transpiration in 1929 were due to higher humidity.

MEASUREMENT OF PHOTOSYNTHESIS

Three methods were employed to determine the rate of photosynthetic activity: that of increase in dry weight devised by Sachs; Sachs' iodine method; and that of determining the total carbohydrate content of the leaves by reduction with picric acid.

In determining dry weight, 100 square centimeters of leaf area were cut from leaves of first-season seedlings. This was done by means of a Ganong's leaf area cutter at each station at 5:00 A.M. and again at 3:00 P.M. These measurements were made on July 10, 1928, which was a cloudless day. The material was immediately placed in an electric oven at 65° C. for a period

of 24 hours, after which it was cooled in a desiccator and weighed. The difference in the weight of the two lots of material, *i.e.*, approximately the increase in carbohydrates, is shown in Table IX.

TABLE IX. *Increase in dry weight of equal areas of leaves during a period of ten hours*

Station and species	Wt. at 5 A.M., mg. per 100 sq. cm.	Wt. at 3 P.M., mg. per 100 sq. cm.	Gain in wt., mg. per 100 sq. cm.	Percentage gain in wt.
Prairie station				
Bur oak	858.1	942.8	84.7	9.87
Hickory	709.5	795.2	85.7	12.07
Red oak	701.6	758.9	57.3	8.16
Linden	334.2	368.8	32.6	9.75
Walnut	484.6	598.8	114.2	23.55
Oak station				
Bur oak	434.6	468.8	34.2	7.86
Hickory	358.9	387.3	28.4	7.91
Red oak	456.8	469.6	12.8	2.80
Linden	266.2	291.3	25.1	9.50
Walnut	212.2	242.8	30.6	14.42
Linden station				
Bur oak	373.4	385.7	12.3	3.29
Hickory	232.1	235.1	3.0	1.28
Red oak	429.2	436.3	7.1	1.67
Linden	217.3	221.5	4.2	1.93
Walnut	169.8	194.9	25.1	14.78

All of the species, except linden and walnut, gave a consistent and marked decrease in photosynthetic output with a decrease in light (Table IX). The shade-enduring linden did quite as well in the oak forest as in the prairie. While the walnut showed a marked decrease from prairie to forest, no further decrease was found in the linden forest. This is rather surprising when it is recalled that walnut is a species commonly considered of only intermediate tolerance to shade (Toumey, '28). The average gain for all species was 12.7 per cent in the prairie, 8.5 per cent at the oak station, and 4.6 per cent in the linden forest.

The leaves were heaviest (*i.e.*, most compact and thickest) in the prairie, much lighter at the oak station, and very light at the linden station. This sequence occurred in each of the 5 species. The average dry weight of 100 sq. cm. of all species in the prairie was 617.6 gm., at the oak station 343.7 gm., and 284.3 gm. in the linden forest.

The dry weight method of determining carbohydrate production is subject to the criticism that 2 sets of leaf samples must be used, and therefore the original weights of the 2 sets may differ. Care was taken to obviate this source of error by obtaining the 2 sets of samples from opposite halves of the same leaves, and also by carefully avoiding the large veins. These data are substantiated, moreover, by those obtained by the other 2 methods.

Typical leaves were collected from first-season seedlings of all 5 species at 5 A.M. and again at 3 P.M. on August 5, 1928. This was a cloudless day.

The chlorophyll was removed by boiling in alcohol, after which a solution of iodine in potassium iodide was applied to determine the relative amounts of starch accumulated in the leaves. All of the species at each station showed only a slight starch content or none early in the morning. By 3 P.M., little starch had been produced at the linden station, a considerably larger amount in the oak forest, and an abundance at the prairie station. The walnut gave a good starch test even in the dense shade of the linden forest. After testing many leaves in this manner throughout the season, it was relatively easy to arrange them into the 5 classes shown in Table X.

TABLE X. *Determination of starch content by Sachs' iodine method*

Station and hour	Bur oak	Hickory	Red oak	Linden	Walnut
Prairie, 5 A.M.....	None	None	None	None	Slight
Prairie, 3 P.M.....	Strong	Good	Strong	Good	Very strong
Oak, 5 A.M.....	Slight	None	None	None	Slight
Oak, 3 P.M.....	Good	Slight	Slight	Slight	Strong
Linden, 5 A.M.....	None	None	None	None	None
Linden, 3 P.M.....	Slight	None	None	None	Good

In the experiments with the picric acid colorimetric method, the photosynthetic activity is based on total carbohydrate content and upon increase in carbohydrate content of leaves after insolation, this being measured as reducing sugars. The method was used as modified by Long ('19, '25, '26).

Ten square centimeters of leaf material were cut with a leaf punch from first year seedlings of each species at each station. The material was taken at daylight and at 3 P.M. on cloudless days during the summer of 1927. At both times 3 separate lots of material were secured. Average results of the triplicate analyses are presented in Table XI.¹

Carbohydrate production was approximately twice as great in the oak woods as in the linden forest (Table XI). In the full sunlight of the prairie

TABLE XI. *Determination of carbohydrate production by the picric acid colorimetric method*

Species	Increase in mg. per 100 sq. cm., in prairie	Increase in mg. per 100 sq. cm., in oak forest	Increase in mg. per 100 sq. cm., in linden forest
Bur oak.....	81.3	31.6	19.0
Hickory.....	83.9	28.8	00.0
Red oak.....	57.7	10.6	7.5
Linden.....	18.2	26.5	4.4
Walnut.....	118.4	25.1	32.1
Average.....	71.9	24.5	12.6

¹ These data were secured by the cooperation of Miss Theodora Klose, to whom a detailed outline of the method was furnished by Doctor Long.

station, it was 5.6 times that at the linden station, and nearly 3 times as great as in the oak forest. The walnut again showed the greatest photosynthetic activity of any of the species at the linden station.

The data obtained by these 3 methods are in substantial agreement. There can be little doubt that the shade of the oak forest, and, even more, that of the linden forest, materially interferes with the growth of forest tree seedlings by greatly reducing the rate of photosynthesis.

Discussion

These experiments indicate that each species studied has a characteristic initial root habit, and thus they are in agreement with the findings of Toumey ('29). The total depth and extent of the roots, however, depend upon the environment under which the seedling develops. If the environment is unfavorable, especially as regards insufficient light, the root system is a miniature of the one that develops under favorable conditions.

It is apparent that soil moisture is not the only controlling factor in the growth of trees at these stations, for the roots of all except linden grew deepest at the prairie station where the moisture content was least. Conversely, the poorest growth of both roots and tops occurred at the linden station where the water content of the soil was greatest. This may seem contradictory to much work recently done on the problem of moisture versus light (Toumey, '28, '29a), but it must be remembered that the conditions for growth were such that moisture was available to seedlings of all species, except the shallow-rooted linden, until late in the growing season. The water relation is a principal factor in the determination of the tree species which occupy various sites on the hillside. This is indicated by the fact that the longest taproots were developed by species such as bur oak which naturally occupy the highest ground. The taproots become successively shorter on species, such as shellbark hickory and red oak, which occupy lower areas; while linden, growing still farther down the slopes, scarcely develops any taproot at all. Thus the type of root appears to be an hereditary adaptation of the species to sites of more or less specific water content.

All of the environmental factors play some part in controlling the growth of tree seedlings. These factors are subject to considerable interplay in their effects upon growth. A factor that is of little consequence during most of the growing season may be of primary importance at some particular time. Thus a hot wind of only a few hours' duration may kill most of the young linden seedlings on an open prairie site. Soil temperature may also be decisive in the germination of seeds and the establishment of seedlings. This factor has been considered of much importance in the physiological activities and growth of seedlings, especially by Bates ('26), Toumey and Neethling ('24), Cannon ('15), Li ('26), and Pearson ('29).

Light and soil water have been generally recognized as of major impor-

tance throughout the growing season. The form of the root system appears to be correlated with the water supply of the soil. The short taproot and numerous laterals of the linden are adapted to the moist but well aerated slopes just above the flood plain. The well developed taproot of red oak and shellbark hickory fits these species for the drier hillsides above the lindens. The vigorous development and extreme length of the taproot of the bur oak explains the ability of this species to occupy the drier slopes and hilltops and to endure drought most successfully. The root system of black walnut combines the deep taproot of the more xeric trees with the strong laterals characteristic of the more mesic ones. This, combined with rapid growth, helps to explain its rather wide distribution as regards water content of soil. That it can make food in rather low light intensities accounts for its distribution on moist slopes along with elm and other tolerant species.

Although root adaptations to water content are significant in an explanation of distribution of forest trees, too much emphasis should not be placed on any one factor. Other factors, especially light, are also of primary importance. From experiments involving the growth of plants in the shade of forests in both trenched and untrenched plots, Fricke ('04), Aaltonen ('26), Craib ('29), Toumey ('29), and others have reached the conclusion that soil moisture is of much greater importance than light in its effect upon the growth of plants under the forest canopy. Thus Toumey ('28) states: "In all ordinary upland forests, the absence of reproduction and other subordinate vegetation is not due to light intensity being reduced to the point where it becomes limiting, but to some other factor, such as available soil moisture. It is only on sites where the available soil moisture or factors other than light are not limiting that the canopy becomes sufficiently dense to make light the limiting factor." Grasse ('29), who worked in white pine forests in Connecticut and New Hampshire, states: "The general conclusion reached is that the intensity and quality of light reaching the forest floor are not the determining factors in accounting for the presence or absence of reproduction in the fully stocked forest where the investigation was made." His work, however, considered survival under reduced light, rather than amount of growth.

This raises the question as to how often and under what conditions available soil moisture is a limiting factor. Craib ('29) agrees with the data presented here that the soil becomes progressively drier in the forest with increase in depth. But he found that forest soils were drier than unforested soils in New Hampshire. This is contrary to the data obtained in southeastern Nebraska, where soils in the linden forest were more moist than those in the oak forest, and unforested soils driest of all. Pearson ('30), working in Arizona, found more moisture at depths of 6-12 inches directly under tree groups than in open places 40 to 50 feet from the trees. Daubenmire ('30) has found that soils in the beech-maple forest in Indiana always have available moisture, but that during much of the summer there is no available water in

the hemlock forest. Apparently it is necessary to discriminate not only between different geographical locations but also between different kinds of forests, when considering the problem of the availability of soil moisture. In southeastern Nebraska, as in Indiana, soil moisture is present in sufficient quantities for continued growth in the deciduous forests, and is not a limiting factor. Whether or not this condition is general in deciduous forests is yet to be ascertained.

That soil moisture can not account for the growth determined in the present experiments is evident from the fact that the greatest growth was obtained in the open prairie habitat where the soil moisture was least and transpiration greatest. Conversely, the least growth was obtained in the dense shade of the linden forest where the water content of the soil was greatest and where transpiration was reduced to a minimum. Clements, Weaver, and Hanson ('29) found that seedlings of *Fraxinus lanceolata*, *Acer negundo*, *A. saccharinum*, and *Gleditsia triacanthos* made a poor growth in moist, lowland, prairie soil, due to competition of the grasses. Growth was even poorer, however, when the seedlings were regularly watered, since the grasses made a ranker growth and cast more shade.

Under these conditions other factors such as light assume a major rôle. When light is reduced below a certain minimum, as in the linden forest, photosynthetic activity is practically stopped. Under such a condition of minimum light intensity, growth is all but impossible, even in tree seedlings. With a somewhat higher percentage of light, as in the bur oak-black oak community, photosynthesis was measurably increased, and growth was correspondingly greater. Maximum growth of tree seedlings, however, was obtained only in the full sunshine of the prairie.

These conclusions regarding the importance of light are in agreement with many carefully conducted investigations. Duration of light has been shown by Weaver and Himmel ('29) to affect greatly the growth of plants both above and below ground. The effects of light intensity upon growth have been fully investigated by Shirley ('29 and '29a), who concludes from greenhouse studies that certain oaks may survive with only one per cent light but are unable to gain appreciably in dry weight. His data show that an increase of light intensity up to 20 per cent gives a proportional increase in growth. He shows also that most plants produce maximum dry matter only in full sunlight, and that root development is always poor under low light intensities. He finds that the light intensity under a forest canopy is almost always so low as to decrease seriously the rate of growth. The researches of Pearson ('29, '30) in Arizona show that trenching benefits seedlings slightly, but that such seedlings do not make the growth exhibited by those in open areas, even when the latter are subjected to considerable competition from the roots of older trees.

Under the conditions of the experiments described in the present paper, the soil moisture was sufficient at all three sites. Light, on the other hand,

differed. It seems reasonable to conclude that an environmental factor, such as light, that is of minor importance under one set of conditions may assume major importance when these conditions are altered. The conflicting data obtained in different parts of the country and under different conditions seem to indicate that extreme caution should be exercised in reaching a general conclusion regarding the relative importance of light and moisture in plant growth. This is imperative at least until much more data have been secured, and data particularly bearing on the physiological responses of plants grown under natural forest conditions.

Summary

Five species of deciduous forest trees were grown in 3 habitats, including the one in which each occurs naturally. The investigations were made in the oak-hickory and linden forests of southeastern Nebraska. They include the development of both roots and tops during the first 3 years, the factors of the environment, and the physiological responses in terms of transpiration, photosynthesis, and growth.

Depth and spread of root systems greatly exceeded height and spread of tops.

The greatest depths attained during the first year were as follows: bur oak (*Quercus macrocarpa*), 5.7 feet; shellbark hickory (*Hicoria ovata*), 2.5 feet; red oak (*Quercus rubra*), 2.4 feet; linden (*Tilia americana*), 1.2 feet; walnut (*Juglans nigra*), 4.5 feet.

The greatest growth was obtained on an open prairie site in full sunlight, and the least in the deep shade of the linden forest. Intermediate rates of growth were found in the oak forest.

Bur oak developed a strong taproot, shellbark hickory and red oak somewhat shorter ones, walnut had a long taproot with extensive laterals, but the linden had a relatively shallow root system.

The form of the root system appears to be correlated with the water content of the soil; the long taproot with strong branches is characteristic of species adapted to drier sites.

The extremes of environmental factors prevailed in the prairie, the most uniform were characteristic of the linden forest, and intermediate conditions obtained in the oak forest.

Transpiration was greatest in the prairie, least in the linden forest, and intermediate in the oak forest. Upland species transpired more vigorously than the less xeric ones of the lowland.

Photosynthetic activity reached a maximum in full sunlight; it was reduced to a very low rate in the linden forest, and was intermediate in the oak forest.

The growth of the tree seedlings was directly correlated with their photosynthetic activity.

Soil moisture was least in the prairie, greatest in the linden forest, and

intermediate in the oak forest. There was available moisture in the soil at all stations except for the prairie station where the moisture was below the hygroscopic coefficient in the surface 6 inches for about 4 weeks in 1927, and in other layers for brief intervals.

Growth was inversely proportional to available water content of soil.

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RACE DETERIORATION IN THE UNITED STATES QUALITATIVELY AND QUANTITATIVELY CONSIDERED

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Quantitatively considered, the continuity of a community, a nation, or a race depends upon the balance between birth rate and death rate. This proposition of course eliminates the question of gains by immigration and the losses by emigration. The excess of births over deaths constitutes the only natural increase of population; and, when the excess falls off, the danger signal shifts to red. The birth rate of France has dropped below the death rate 1.5 per thousand of population. In England in 1928 it was less than 5 per thousand above the death rate. In the United States, within a period of less than a quarter of a century, the birth rate has dropped from 25 to less than 19 per thousand of population. The type of civilization toward which we are drifting is not conducive to the only natural means of the increase of population and the preservation of the race.

Qualitatively viewed, the continuity of a people depends upon quite another factor—namely, the preponderance of men and women of profound and broad mentality. It is the few who are possessors of wisdom and leadership, and not the *hoi polloi*, that make a nation both great and strong. In the light of history a people may retain a racial or national name and yet have lost the characteristics that made them famous. Greek peoples still exist in name, but the Greeks of today are not the descendants of the old Homeric stock, the Greeks whose greatness created an unparalleled center of art and literature. The riddle of Hellenic decline is found in the low birth rate of the Homeric class and the high birth rate of the illiterates. The modern Greeks are the descendants of Helots. The stock that made old Greece a great nation bred itself out of existence and left the fate of a nation to the offspring of illiterates.

The Italians of the present time are not the descendants of such Roman families as the Corneli, the Gracchi, and the Fabricii; they are the offspring of proles and of slaves of various races—very largely the captives of war. The old Roman families disappeared because of a birth rate much below that of the illiterates. The cross-breeding of diverse races produces not the higher but the lower intellectual type. A mongrel people has never yet attained real greatness.¹

As a nation, the United States presents race problems that do not exist elsewhere. Seventy-five nationalities are represented in its population and

¹ Gould: America, A Family Matter.

these include practically every race. The Aryans represented in the United States include Mediterraneans, Alpines, and Nordics. They are prolific in the order named. When Mediterraneans and Nordics cross the Nordic element is gradually bred into numerical insignificance, or is bred out of existence altogether.²

Northwestern and much of central Europe present no such problem. The Scandinavian countries are purely Norse; England is Anglo-Saxon and Nordic; Germany is Teutonic and Nordic—all after many centuries and generations. The race problem does not exist among these peoples except as it may be the struggle between the intellectuals and the illiterates. The latter are the prolific breeders. In the United States the race problem is the greatest of all problems. Here, the descendants of Mediterraneans are increasing in a ratio far greater than are the Nordics. Here and there the birth rate of the foreign-born is almost twice as great as that of the Nordic stock; the Anglo-Saxon element of population has become almost insignificant in number. The original stock is being bred out of existence.

President George Barton Cutten of Colgate University has reduced certain comparative rates from the census of 1820 to proportionate figures. He finds that the average number of children per family in the United States of native-born parents is 3.0; of Polish and Italian immigrants, 4.5; of Hungarians, 4.2.³ Dr. Cutten computes the descendants of 1,000 Harvard graduates in 200 years at 50, while the descendants of the same number of southern Europeans in the same time will number approximately 100,000.

Granted that many things in the meantime may occur to change the present rate of increase of intellectuals over non-intellectuals of Nordic descent, the obvious fact remains that the descendants of foreign-born, non-Nordic peoples of inferior intellectual type are increasing in far greater proportion than are those of Nordic ancestry. As Dr. Cutten has clearly and tersely put it, "Brains are bred from brains and not from non-brains." Education is usually regarded as the panacea and cure-all for social and intellectual short-comings. But education does not overcome heredity; moreover, a quart container cannot be educated to hold half a gallon. The melting-pot cure is a pleasant delusion bearing very pretty paper flowers; but a few years in an elementary schoolroom will not accomplish the results for which Dame Nature requires 15 or 20 centuries.

Let us again look at the case quantitatively. Of the three great educators, the schoolmaster, the domine, and the doctor, the last-named has accomplished results that are marvelous; moreover, the doctor's results are concrete. Most of the communicable diseases have been conquered or, at least, are on the straight way to conquest. Typhoid fever and diphtheria are almost eliminated. Because of this conquest in 50 years, the death rate in the United States has been lowered approximately one-half. Since 1900 it has been

² Stoddard: *The Revolt Against Civilization*.

³ Cutten: *Mind—Its Origin and Goal*.

reduced from 17.6 per 1,000 of population to a rate of 12.1. In less than 30 years the rate of infant mortality has been lowered from 126 to 67 for each 1,000 born.

The great gain in the salvage of infant life has created a change in the statistics of the average span of life, but the nature of the change has been misunderstood. A metropolitan newspaper, commenting upon the case, declared that an average of 18 years had been added to the expectation of life. Such a statement is a most mischievous fallacy. Because of the conquest of communicable diseases incident to child life, a far greater proportion of young children are started on the race for a goal of 50 years, but the gain already is nearly offset by the cumulative losses from the deterioration ailments that vex humanity beyond the age of 50 years. The first of the following tables was prepared from the mortality statistics of the Bureau of the Census; the second was computed by a life insurance company:

TABLE I. *Life expectancy for 1910 and 1920, from the Bureau of the Census*

Year	Sex	At Birth	At 32 Yrs.	At 62 Yrs.
1920	M	53.98	34.93	13.38
1910	M	50.23	33.33	12.85
	Gain	3.75	1.60	0.53
1920	F	56.33	36.12	14.01
1910	F	53.62	35.40	13.70
	Gain	2.71	0.72	0.31

From 1910 to 1920 the maximum gain is less than four years; at the age of 62 years it has fallen to six months in the case of males and to four months in the case of females. All this shows that the claims of a vastly greater expectation of life are preposterous.

Several years must pass before the statistical tables of the Bureau of the Census for 1930 can be computed, but the figures of the life insurance company afford a significant comparison:

TABLE II. *Life expectancy for 1921 and 1927, from life insurance company figures*

Year	At 37 Yrs.	At 47 Yrs.	At 57 Yrs.	At 67 Yrs.
1927	31.47	27.51	16.57	10.60
1921	32.86	28.90	17.52	11.50
Loss	1.39	1.39	0.95	0.90

These figures indicate that the gain in the span of life due to the control of communicable diseases will have disappeared within the course of a few years—probably before 1940. Why the loss? A study of mortality statistics for the past 30 years or more gives the answer—namely, the rapid in-

crease of the deaths incident to old age; and, for the greater part, they are due to degenerative causes. They are accelerated by modern environment, the decaying influences of modern civilization.

Foremost among them are heart and artery diseases. In 1900 the death rate for each 100,000 of population was 111; in less than 30 years it has increased to 209. As a matter of fact, about one death in every six is due to one or the other of these causes. The physician may prevent deterioration; he may arrest it; but he cannot replace worn-out valves, nor can he restore them to health. The death rate from heart and artery ailments is greater in urban than in rural communities. It is the strenuous life forced upon humanity by modern civilization and its environment.

To the list of other bodily ailments responsible for heart deterioration, the psycho-neurotic factor is always present; it cannot be ignored. Ever since the human animal has been the conscious possessor of a heart, he also has been conscious of the fact that it reacted to the "emotions." Hence the time-worn saying of our forebears—"the heart is the seat of the emotions." There is more than a bit of truth in the opinion of 25 centuries. Modern education, a product of the civilization of the present time, counsels us to restrain our emotions; modern business forces the issue.⁴ Thereby additional strain is put upon the heart. "The tendency to death from heart disease," declares Dr. W. J. Mayo, "is common among all men who live lives of hard stress in which control of the emotions is necessary." The urban man is usually under constant strain. Before those with whom he conducts his affairs he must preserve a mental poise; he cannot give way to his emotions. His heart suffers in consequence.

Cancer, the problem upon which medical science is concentrating its energies, is a disease of modern environmental conditions—of super-civilization. It is distinctively an old-age ailment. Before the age of 30 years the mortality therefrom is almost negligible. In the United States the death rate at 70 years is about 12 times as great as at the age of 40. In 1900 the rate was 60.7 for each 100,000 of population; by 1927 it had increased to 95.6. Neither the cause of a most fatal disease is known, nor has a cure for it been found. Medical science is ignorant even of the means of prevention.

Apoplexy, the cerebral hemorrhage of the physician's vocabulary, stands a varying third as a cause of death. Since 1900 the rate has advanced from 69.0 to 85.7. Unlike the prognosis of heart ailments, the fatalities of apoplexy are greater in rural than in urban communities—perhaps in part for the reason that the life and the surroundings of rural dwellers are more favorable to a generous nourishment and therefore the body develops a greater blood supply. Approximately three-fourths of the deaths from apoplexy occur after the age of 45 years.

⁴ To a certain extent, striated or "striped" muscular tissue is subject to conscious control. The muscular tissue of the heart is a primitive form of striated muscle.

Bright's disease, or chronic nephritis, presents an interesting problem. From an average rate of 88.2 for the five years ending 1904, the rate reached a peak of 101.6 in 1915. For a few years thereafter it fell off rather sharply. Why the lowering of the death rate? Who knows. Bright's disease is still one of the principal causes of decedence among people past 50 years of age. Rheumatism, diabetes, and ailments of the liver add to the number of diseases that indicate physical and physiological degeneration, and the total is nearly one-half the yearly mortality. If to these we add the deaths from influenza, pneumonia, and tuberculosis, which, though not degenerative ailments, are highly fatal to elderly people, the deaths from old-age ailments will considerably exceed one-half the yearly mortality.

The only unpreventible cause of death is old age, the time when the clock has run down. Were the deaths from degenerative ailments decreasing the mortality from senility would be increasing. As a matter of fact, the rate from senility is decreasing. In the five years ending 1904 the rate was 41; in the five years ending 1925 it was not quite 12.

Should the yearly increase of deaths from degenerative diseases and the growing rate of deaths from violent causes continue for the next decade, it is evident that the gains of population from births and from the arrest of communicable diseases will be overcome. In time, perhaps, medical science may discover preventive measures against degenerative ailments. Certainly at the present time they have the upper hand and ride rough-shod. To discover prevention is one thing; to put it into practice is quite another. Civilized humanity is hard-riden by its social environments.

All the foregoing cases hark back to a general problem that is most difficult of solution—namely, the conflict between our social and our biological inheritances. Among primitive peoples the problem did not exist. The problems of social environment did not worry the neolithic man into cardiac failure. Among moderns the conflict between social and biological inheritances is intense and the environment is correspondingly severe. It is growing more complex also as the years go on. Modern civilization is the sum total of our social inheritances. But while the evolution of our biological inheritances proceeds so slowly as to seem negligible, the evolution of our social inheritances and the conditions that go with it may be measured in terms of years. As a result, the man of fifty is losing out. His span of life is growing shorter instead of longer. There is too much steam pressure for the boiler.

SUMMARY

In the United States, the mixture of 75 races, and the higher birth rate of races of low intellectual capacity as compared with the higher intellectual stock, is causing race deterioration.

Deaths incident to old age, mostly from degenerative diseases such as

those of the heart and arteries, of the kidneys, and cancer, are increasing owing to the pressure of the environment created by modern civilization. The increase is greater in city than in rural populations. The expectancy of life at 47 years has decreased from 28.90 in 1921 to 27.51 in 1927, or 1.39 years.⁵

⁵ Except as noted, the foregoing rate figures are taken from the mortality statistics of the U. S. Bureau of the Census.

A COMPARISON OF TEMPERATURES IN WIDELY DIFFERENT ENVIRONMENTS OF THE SAME CLIMATIC AREA ¹

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INTRODUCTION

The ecologist who is interested in studying the relationship between climatic areas and the geographic distribution of plants and animals is practically forced to accept the Weather Bureau data as to the physical characteristics of the climatic areas in question. The Weather Bureau stations are usually on the tops of buildings in cities, while the organisms in which the ecologist is interested are distributed over the natural habitats of the area. The ecologist who is interested in studying plant succession and its influence upon the physical characteristics of the immediate environment, finds certain evidence that the physical characteristics of these environments undergo a progressive change from the initiation of succession on bare areas to the climax forests. With these considerations in mind it seemed worth while to make a study of certain of the physical factors in a series of environments representing the various stages of ecological succession in a climatic area where the environments could be compared with 2 Weather Bureau stations. This study has been made to include a period of 6 weeks representing the hottest part of the year, which is, incidentally, one of the most important growing periods.

LITERATURE

There are few thorough-going studies which compare temperature values of contrasting environments in the same climatic area. If ecological literature is searched, numerous data will be found which relate temperature to the flora or fauna in a given environment, but these scattered data cannot be brought together to give a comparison of one environment with another because they are not concurrent as to time, place or method.

Pioneer studies on the influence of forests on air temperature were made by Schubert (1897) at Eberswalde in Germany. His studies extended through the warmer 6 months of the year and consisted of daily 2 P.M. readings made with an aspiration thermometer in a pine forest, a beech forest and an open field. He found that during July to August inclusive the pine forest averaged 0.3° C. and the beech forest 1.1° C. cooler than the open field at that hour. When the 6 month period from April to October is considered

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the pines still average 0.3° C. cooler than the open field but the beeches average only 0.7° C. cooler, due to the fact that their foliage is not at a maximum early and late in this period.

Müttrich in 1900 published a very reliable comparison of air temperatures of a pine forest and an open field at Eberswalde made over a period of 8 years in both forest and field stations. Daily, monthly and annual means were based on bi-hourly readings from the thermograph records. In this the investigator used the hourly method of taking temperatures to calculate the means recommended by Hartzell ('19) 2 decades later. A summation of air temperature for the 8 year period is given by months and by hours for field and forest. Particularly interesting is the table giving the temperature difference between field and forest at each hour of the day for each month. This table shows in a graphic way that the temperature of the air in the open field becomes higher than that in the forest during the course of the day, but that the open field is cooler than the forest at night. The mean temperature of the forest for the entire 8 years was 7.68° C. as compared with 7.95° C. for the field. Müttrich points out that the means of forest and open field do not deviate as much as their maxima.

In this country Pearson ('13) has contributed the most clearcut comparison between forest and open field temperatures. His yellow pine forest showed an annual mean 2.7° F. higher than that of the adjacent open park, in contrast to the findings of Müttrich in Germany. Pearson's studies were made at an altitude of approximately 7,250 feet, however, in a region quite different from that at Eberswalde, and his temperatures are based upon daily maxima and minima. In the case of this comparison the minima of forest and open are more widely separated (average 6.4° F. for the year) than the maxima (average 0.9° F.). The mean daily range is 7.3° F. less in the forest than in the open. The investigator believes that the generally higher temperature in the forest is due more to the deflecting of cold air currents from neighboring mountains by the trees than to the checking of heat radiation from the forest by the tree crowns. Soil temperatures in the forest and in the park were investigated for July to October inclusive and found to be 5.0° F. lower in the forest at a depth of 2 feet.

Pearson ('20) made a study of air temperatures in different forest types at different altitudes in the San Francisco Mountains in Arizona. His 5 stations ranged in altitude from 5,000 to 11,500 feet. These studies give more of an indication of the effect of different altitudes than of the influence of the several forest types on air temperature.

The comparisons of different strata of a single environment has been the object of several published investigations. Allee ('26) has compared the temperatures of the surface and aerial strata of a tropical rain forest. Weese ('24) has compared the 6 centimeter soil stratum with the 0.6 m. and 10.0 m. aerial strata throughout the entire year in an elm-maple forest. Chapman, Mickel, et al ('26) have published some data on soil temperatures at various

depths on a sand dune in Minnesota. For desert regions McKenzie-Taylor and Burns ('24) have made rather complete studies of temperature in the different soil strata. Their results are very beautifully shown by means of soil isotherms. Swezey ('03) made a study of soil temperatures at 7 different depths over a period of 13 years at Lincoln, Nebraska.

Relative to the importance of a knowledge of the variance of the physical factors of different environments it may be stated that these are usually considered the principal factors in the determination of flora and fauna. Shelford ('12) has concluded that changes in animals during plant succession are due more to the changes in the physical factors than to changes in the flora as such. Sanderson and Peairs ('13), Headlee ('14) and Pierce ('16) were among the earlier workers who illustrated clearly the importance of the temperature factor to insect development. The relation of temperature to plant growth is well recognized by students of plant associations. Livingston ('16) has proposed a system of physiological temperature indices for the study of plant growth in relation to climatic conditions. Sampson ('18) has computed temperature summations and presented physiological temperature coefficients in considering plant growth in certain vegetative associations.

Perhaps the paucity of significant comparisons of the temperatures of different environments published is due very largely to the difficulty of interpreting such data after they have been obtained. Harris, Kuenzel and Cooper ('29) have pointed the way for the treatment of such data. They illustrate the use of regression lines on correlation surfaces, and of statistical constants for comparing simultaneous or associated pairs of measurements.

The comparison of temperatures in different local environments is not unrelated to various aspects of the broader problem of geographical distribution. Comparisons by climographs, such as those of Taylor ('16) commonly employed in the broader studies, can be applied to the study of restricted environments in certain cases. Many of the laws which are concerned with geographical distribution, as those of Merriam (1894, 1898), Sanderson ('08) and Hopkins ('18), can be applied advantageously to individual local habitats.

DESCRIPTION OF THE ENVIRONMENTS

The stations studied were all located in the Minneapolis, St. Paul, Anoka and White-Bear quadrangles bounded by the meridians 93° and $93^{\circ} 30'$ and the parallels $44^{\circ} 45'$ and $45^{\circ} 15'$. This is in the upper Mississippi subprovince of the Glaciated Plains. The stations were located at an altitude of 900 to 940 feet above mean sea level, and the altitude of the quadrangles varies from 700 to 1,180 feet above sea level.

The Sand Dunes were located in Anoka County in an intramorainic plain characterized by low sand dunes, marshes and lakes. The surface is sand without boulders, pebbles or clay-beds. The instrument shelter in this case was placed on a very large blow-out where it was completely exposed to wind and sun (Fig. 1).

The Tamarack Bog was located in Anoka County approximately 15 miles due east of the City of Anoka. It is a typical swampy area in a region of intramorainic plains. The instrument shelter was placed in a dense portion

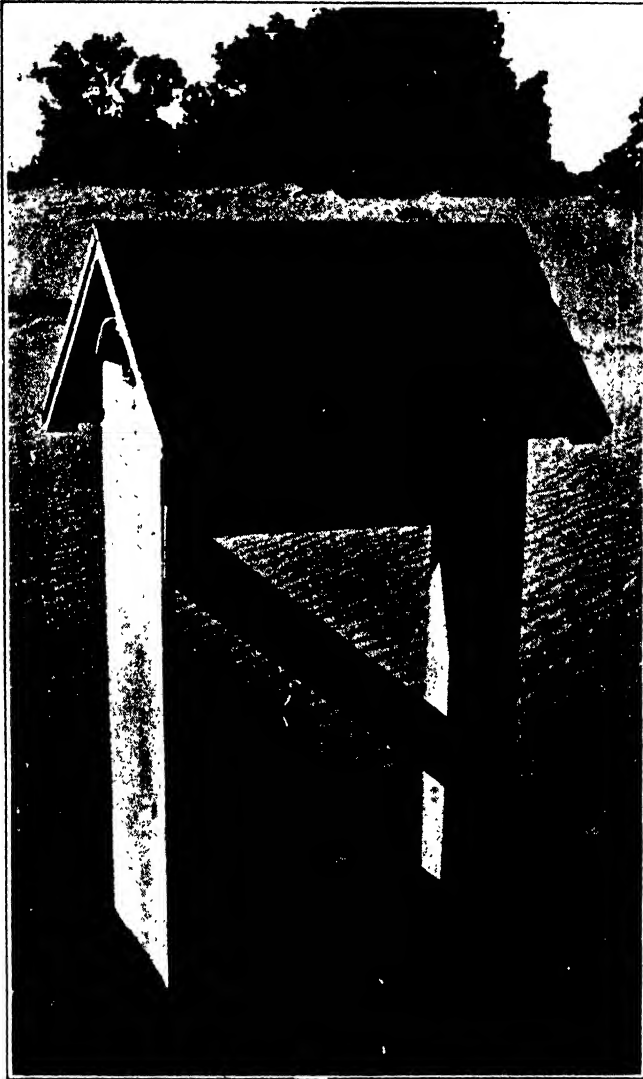


FIG. 1. Instrument shelter on sand dune.

of the bog where the Tamaracks (*Larix laricina*) shaded the shelter so that the direct sunlight could not fall on it during any period of the day.

The Pine Plantation is a 14 year old planting of Scotch Pine (*Pinus sylvestris*) and Jack Pine (*Pinus banksiana*) north of Lake Vadnais in Ramsey County. In this case the instrument shelter consisted of a wooden box

36 x 18 x 18 inches covered with white oil-cloth. The box was open only on the north side, and the instrument was about 3 feet from the ground. Checks showed no significant temperature differences between this and the other instrument shelters used. The shelter was shaded by trees so that the direct light of the sun never fell on it.

The Oak Forest is located in Ramsey County, 0.5 mile east of Lake Johanna. It is a typical mixed oak forest with the red oak (*Quercus rubra*), the burr oak (*Quercus macrocarpa*) and the white oak (*Quercus alba*) dominating. The shelter was placed so that it was shaded most of the day.

The Basswood-Maple Forest is located in Hennepin County in the west-central portion of Minnetonka township. The surface is an undulating glacial moraine. The forest is the regional climax with the basswood (*Tilia americana*) and the maple (*Acer saccharum*) dominating. The shelter in this case was placed so as to be shaded throughout the day.

The Weather Bureau stations are located in the business sections of the cities of Minneapolis and St. Paul.

THE INSTRUMENTS AND SHELTERS

The temperatures were recorded with standard recording hygrothermographs manufactured by Julien P. Friez and Sons. The records were changed weekly, and the instruments were checked for time and temperature on the day the record sheet was changed and once during the week.

The shelters were made especially to meet our requirements. Briefly they consisted of white pine with the instrument cabinet 12 x 12 x 24 inches with two sides of the shelter covered with a very coarse wire lath so that the circulation of the air was not impeded. The shelter was roofed so that water could not enter even in the most severe storms. Care was taken in construction that no pockets of dead air could accumulate (see Fig. 1).

COMPARISONS OF THE MEAN DAILY TEMPERATURES

For the pine plantation, mean daily temperatures were available for April, May and June. These are given as degree-hours above zero Fahrenheit. Mean daily temperature can be obtained by dividing by 24. From the data the mean weekly temperatures were calculated and plotted in comparison with the same data from the St. Paul and Minneapolis Weather Bureau as in fig. 2. It is seen that the 2 Weather Bureau temperatures are very closely comparable with each other, as would be expected. With the exception of the first and the ninth weeks, the pine station temperatures are very closely comparable to the Bureau figures. These 2 weeks lacked data for several cooler days, and are consequently a little higher than they would otherwise be. Between these two very different kinds of environments then, direct comparison of daily temperatures is not useful as showing environmental temperature differences.

Harris et al ('29) have recently indicated the usefulness of the correlation method for the comparison of the physical factors of habitats. Taking the 3 most different of our 5 environments, namely: the basswood-maple climax forest, the tamarack bog, and the sand dunes, we have applied their method

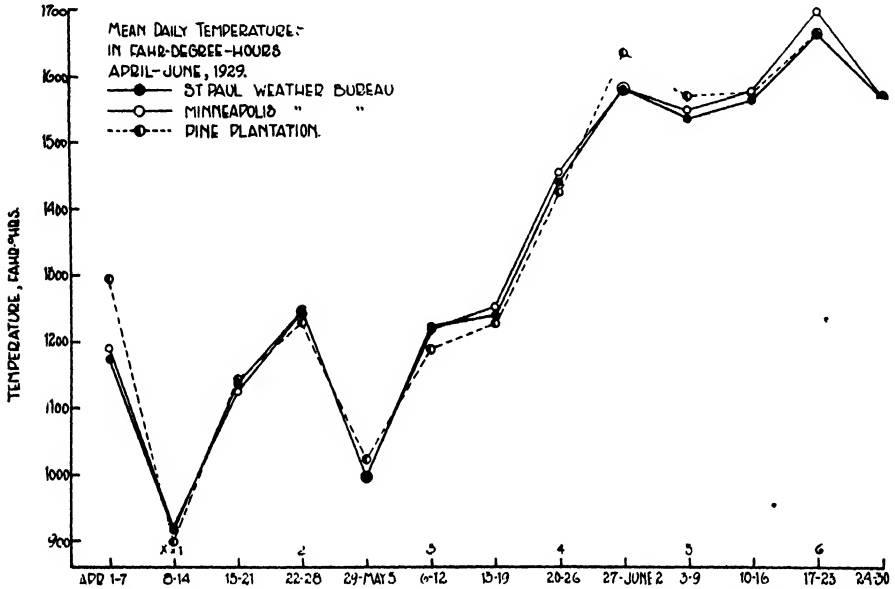


FIG. 2. Mean daily temperatures in Fahrenheit-degree-hours for the Weather Bureaus at St. Paul and Minneapolis and for a pine plantation.

with some slight modifications. The mean daily temperatures from July 2 to August 12 inclusive were first calculated from the thermograph tracings by summing the temperatures at even hours and dividing by 12, thus avoiding inaccuracies inherent in the method of using maximum plus minimum divided by 2. Correlating these daily means for the 3 possible pairs by the Pearson product-moment formula

$$r_{xy} = \frac{\frac{\Sigma(xy)}{N} - \bar{x}\bar{y}}{\sigma_x\sigma_y},$$

(where \bar{x} and \bar{y} are means of distributions) we obtain:

Basswood—Dunes	$r = .914 \pm .019.$
Basswood—Tamarack	$r = .902 \pm .022.$
Tamarack—Dunes	$r = .904 \pm .023.$

These very high correlations indicate that the temperatures in the different environments varied together in closely parallel fashion, but do not indicate the most probable temperature of one environment when another environment

is at some given temperature. This must be shown by regression formulae plus graphs. These regressions were calculated by the formula

$$x = \left(x - r_{xy} \frac{\sigma x}{\sigma y} \bar{y} \right) + r_{xy} \frac{\sigma x}{\sigma y} y.$$

Let B represent the mean daily temperature at the basswood-maple forest, D that at the dunes, and T that at the tamarack bog, the bars representing means of distributions of mean daily temperatures, we find the following regressions:

$$\begin{aligned} B &= 71.17 + .676(D - \bar{D}); & \bar{D} &= 72.83. \\ D &= 72.83 + 1.240(B - \bar{B}); & \bar{B} &= 71.17. \\ T &= 70.82 + .768(D - \bar{D}); & \bar{D} &= 73.71. \\ D &= 73.71 + 1.176(T - \bar{T}); & \bar{T} &= 70.82. \\ B &= 71.18 + .830(T - \bar{T}); & \bar{T} &= 70.18. \\ T &= 70.18 + 1.084(B - \bar{B}); & \bar{B} &= 71.18. \end{aligned}$$

(The discrepancies in the means of distributions is due to the fact that the same identical pairs of daily means were not available for all pairs of environments.) These regression lines are plotted in pairs in figure 3. To facilitate comparisons, all the regressions are plotted as of y on x . In each graph, the broken line labeled " $y=x$ " is the "line of equality" to use Harris' phrase—along this line the temperature of whatever environment is on the vertical ordinate is the same as the temperature in whatever environment is on the horizontal abscissa. The full lines are the regression lines, indicating the generalized relationship between the mean daily temperatures of the given environments. The letter pairs (e.g., $B-D$, $D-T$) indicate the environmental pairs as above. The numerical figures on ordinates and abscissae are mean daily temperatures.

Consider first separate regression lines in relation to the line of equality. The regression line crosses the equality line at a point where the mean daily temperatures of the 2 environments are the same. In the case of each pair of environments the regression of each member is calculated on the other so that 2 regression lines are obtained. Since the correlation between the temperatures of environments is not perfect (albeit high) we find a discrepancy in the points at which the 2 regressions cross the line of equality, but the discrepancy is not great in the case of any pair, and the relative lowness or highness is not disturbed. We find (from the $T-D$ and $D-T$ lines) that the tamarack bog and the dunes resemble each other on relatively cool days, with a mean of below 63° F., temperatures for the most part below our graphs. The dunes are practically always warmer than the bog except on days when the dunes fall below 63. From the $B-D$ and $D-B$ lines it is seen that the basswood-maple forest and the dunes are alike on somewhat warmer days, with mean temperatures of 64 to 68. The bog and the forest ($B-T$ and $T-B$ lines) are brought to the same condition on rather warm days having a mean tem-

perature of 77 to 81. On cooler days the forest is warmer than the dunes.

From the fact that lines involving all 3 environments (see any of the figures) never cross the equality line at the same point it can be said that, gen-

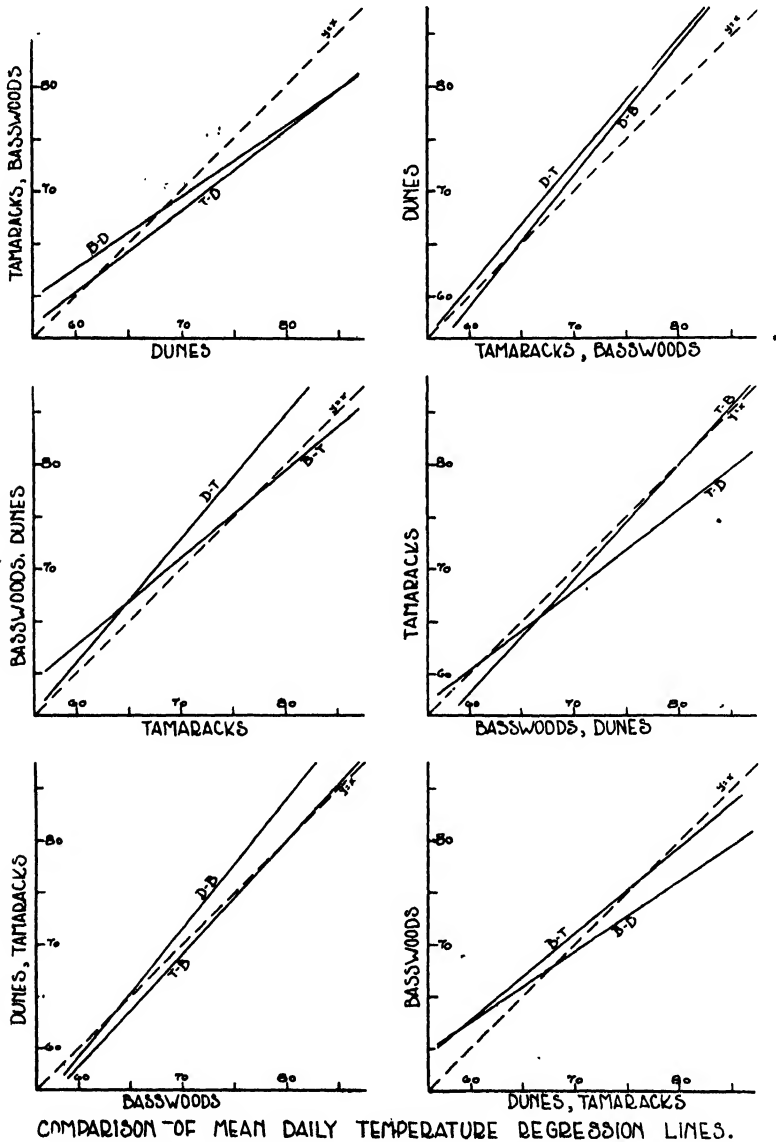


FIG. 3. Comparison of mean daily temperature regression lines at 6 stations.

erally speaking, at no temperature are all 3 environments at the same mean daily temperature. But by considering pairs of regression lines (as plotted) we can see when 2 environments are at the same temperature for a somewhat

similar temperature of the 3 others. In other words, we may see what mean temperature is produced in one place by conditions that will bring the other 2 places each to a temperature the same between themselves, resulting in 2 mean temperatures among the 3 places. From the first 2 graphs we see that the conditions resulting in hot to very hot days at the dunes—at 85° F. or above—will bring both the forest and the bog to a mean temperature of 80. On cooler days at the dunes the forest is warmer than the bog. From the last 2 graphs it is seen that conditions resulting in very cool days (for this season) at the forest, with means at 62 or below, will bring the dunes and the

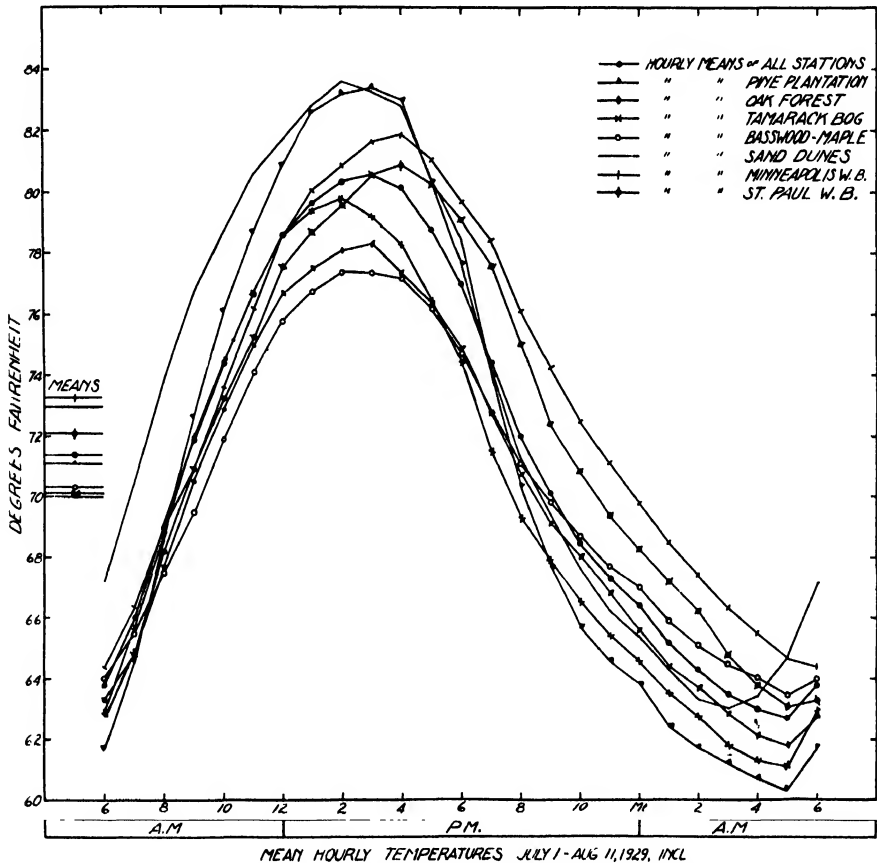


FIG. 4. Mean hourly temperatures July 1 to August 11, 1929, inclusive, at 8 stations.

bog to a mean of 59 or below. On warmer days at the forest the dunes are warmer than the bog. As a corollary of these relationships—on warm days the dunes are the warmest, on cool days the forest is the warmest. From the second pair of graphs it is seen that conditions resulting in a moderately cool day at the bog, with a mean varying little from 65, will bring the forest and the dunes to a mean of 66.5—such conditions bring all 3 places to very nearly

the same mean. On warmer days at the bog the dunes are warmer than the forest—on cooler days the forest is warmer than the dunes.

COMPARISONS OF THE MEAN HOURLY TEMPERATURES

In comparing the temperature changes during the day, the mean hourly temperatures were calculated for each hour of the day for the 6 weeks from July 1 to August 11, 1929, inclusive, for the 5 field stations and the 2 Weather Bureau stations, and from these the mean of all of the stations was calculated. These means are given in Table I and may be compared in the diagram (Fig. 4). The means show great variation among themselves. The ranges of the mean hourly temperatures are :

Minneapolis Weather Bureau	17.5° F.
St. Paul Weather Bureau	17.5
Pine plantation	23.1
Sand dunes	20.6
Tamarack bog	18.7
Oak forest	16.5
Basswood-maple forest	13.9
All-station average	17.9

It is seen that the ranges of the Minneapolis and St. Paul stations are very close to the all station average range. The average range of the field stations is 18.6° which is a degree greater than the range of the Weather Bureau stations.

TABLE I. *Mean hourly temperatures, in degrees F., for the 6 weeks July 1 to August 11, 1929, inclusive*

Hour	St. Paul Weather Bureau	Mpls. Weather Bureau	Tam- arack bog	Sand dunes	Pine plan- ta- tion	Oak forest	Bass- maple forest	All- station average
Mt.	68.3	69.8	64.6	65.4	63.8	65.6	67.0	66.4
1	67.2	68.5	63.5	64.3	62.4	64.4	65.9	65.2
2	66.2	67.4	62.7	63.3	61.7	63.7	65.1	64.3
3	64.8	66.3	61.8	63.0	61.2	62.8	64.5	63.5
4	63.8	65.5	61.3	63.4	60.7	62.1	64.0	63.0
5	63.1	64.7	61.1	64.7	60.3	61.8	63.5	62.7
6	63.3	64.4	62.9	67.2	61.7	62.8	64.0	63.8
7	64.8	66.3	65.7	70.4	64.6	64.9	65.5	66.0
8	68.2	69.0	68.8	73.8	68.6	67.7	67.5	69.1
9	70.9	70.9	72.0	76.7	72.7	70.5	69.5	71.9
10	73.3	73.6	74.5	78.7	76.1	72.9	71.9	74.4
11	75.3	76.2	76.7	80.6	78.7	75.0	74.1	76.7
12	77.6	78.6	78.6	81.7	80.9	76.7	75.8	78.6
1	78.7	80.1	79.4	82.8	82.6	77.5	76.8	79.7
2	79.6	80.9	79.8	83.6	83.2	78.1	77.4	80.4
3	80.6	81.7	79.2	83.3	83.4	78.3	77.4	80.6
4	80.9	81.9	78.3	82.8	83.0	77.4	77.2	80.2
5	80.3	81.1	76.5	80.4	80.4	76.4	76.2	78.8
6	79.1	79.7	74.4	78.4	77.7	74.9	74.7	77.0
7	77.6	78.4	71.5	74.1	74.0	72.7	72.8	74.4
8	75.0	76.1	69.3	71.3	70.3	70.7	71.1	72.0
9	72.4	74.2	67.9	69.4	67.7	69.1	69.8	70.1
10	70.8	72.5	66.5	67.5	65.7	68.0	68.7	68.5
11	69.4	71.1	65.4	66.2	64.6	66.8	67.7	67.3
Average	72.1	73.3	70.1	73.0	71.1	70.0	70.3	71.4
Range	17.8	17.5	18.7	20.6	23.1	16.5	13.9	17.9

The spread of temperatures among the 7 stations is nearly the same at all hours of the day. In the morning from the hours of 6 to 8 the stations are within 2 degrees of each other, save for the sand dunes which begin to have a rise of temperature at 4 A.M. which is 2 hours before any of the other stations. The dunes are higher than the other stations until 2 P.M. when they fall rapidly. The Weather Bureau stations are higher than the others from 5 P.M. until 4 A.M. This is probably due to the fact that the city streets accumulate considerable heat during the day which is given off during the night, with the result that the city temperatures are higher than the rest of the stations during the night.

The hourly variation may be indicated by the use of the standard deviation of all of the stations rather than by using their differences. The standard deviation is found by using the formula

$$\text{S.D.} = \sqrt{\frac{\sum(x^2)}{N} - \bar{x}^2}$$

where x^2 is the square of the station deviation from the all-station average for the given hour and \bar{x}^2 is the square of the all-station average for the particular hour and N is the number of stations being compared. These hourly standard deviations are plotted in figure 5. The greatest deviation is found to come at

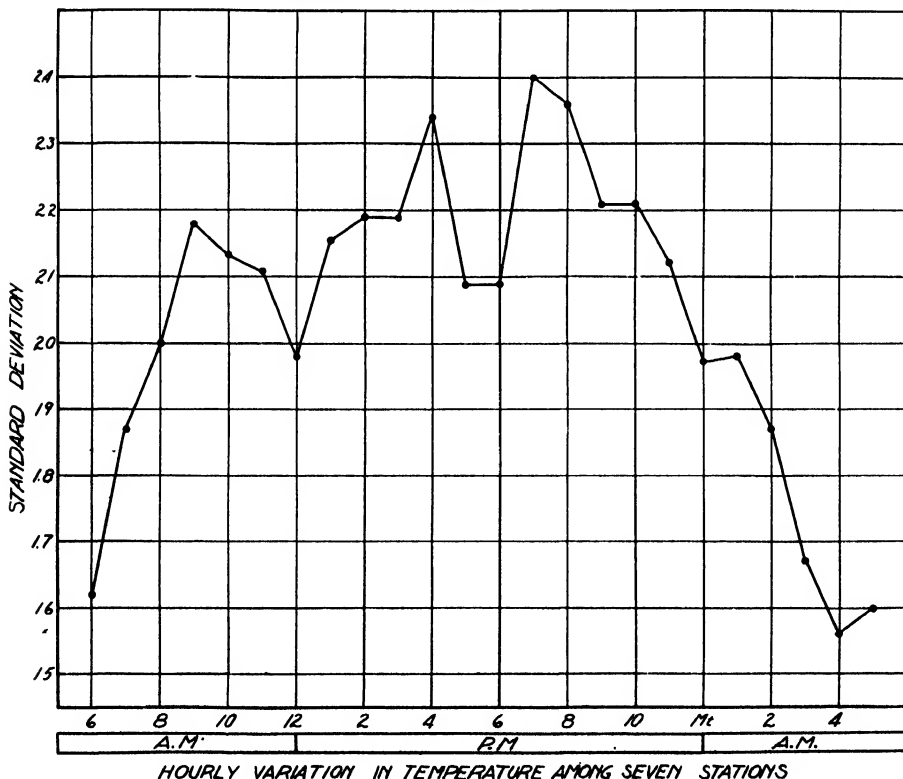


FIG. 5. Hourly variation in temperature among 7 stations.

7 P.M. and the least deviation at 4 A.M. This is what might be expected, since during the day when the heat of the sun is being intercepted by the varying degree of coverage of foliage, the temperatures in the shelters which are only a few feet above the ground would be subject to considerable variation among themselves. At night with the source of heat removed, the stations would tend to come to an equilibrium with little deviation between stations.

The actual mean temperatures for the 6 weeks at the field stations are lower than the mean temperatures for either the Minneapolis or the St. Paul Weather Bureau Stations, save in the instance of the sand dunes which is almost coincident with the Minneapolis station. Merriam (1898) has divided the continent of North America into life zones on the basis of the Northern and Southern limits of distribution according to temperature. He states that animals are limited in their southern range by the mean temperature

TABLE II. *Temperatures, in degrees C., recorded simultaneously in the various strata of the different environments*

	Air		Soil				
	5 ft.	6 in.	Surface	1 in.	6 in.	12 in.	18 in.
Basswood-maple forest							
July 10, 3 P.M.	26.5	25.0	24.7	19.5	16.5	16.0	15.0
4 P.M.	25.5	24.7	22.5	18.5	16.5	16.0	15.0
5 P.M.	24.5	24.0	23.5	18.5	16.5	16.0	15.0
July 15, 2 P.M.	27.0	25.0	26.0	18.0	17.0	16.5	16.0
3 P.M.	22.5	23.0	25.0	18.0	17.0	16.5	16.0
4 P.M.	24.0	24.5	24.5	18.5	17.0	16.5	16.0
Average	25.0	24.4	24.4	18.5	16.7	16.2	15.5
Tamarack bog							
July 10, 3 P.M.	26.5	25.0	22.0	22.0	18.0	16.0	15.0
4 P.M.	26.2	25.0	22.7	21.0	—	16.0	15.0
5 P.M.	26.0	24.4	20.0	—	—	—	—
July 15, 2 P.M.	25.8	25.5	23.0	20.5	17.5	16.0	15.5
3 P.M.	25.5	25.0	23.0	20.5	17.5	16.0	15.5
4 P.M.	26.0	25.0	23.0	20.5	17.0	16.0	15.0
Average	26.0	25.0	22.3	21.0	17.4	16.0	15.1
Oak forest							
July 10, 3 P.M.	25.6	25.5	21.6	18.7	17.2	16.1	15.3
4 P.M.	26.0	25.3	21.1	18.0	16.8	15.9	15.3
5 P.M.	25.6	25.6	18.8	18.0	16.2	15.6	15.2
July 15, 2 P.M.	25.0	25.0	22.1	19.3	18.0	17.3	16.4
3 P.M.	25.0	25.3	22.0	19.4	18.3	17.2	16.3
4 P.M.	25.0	25.5	21.0	19.7	18.2	17.0	16.2
Average	25.4	25.4	21.1	18.8	17.4	16.5	15.8
Pine plantation							
July 10, 3 P.M.	27.5	28.7	28.9	22.0	21.0	19.0	19.0
4 P.M.	28.5	27.7	28.0	22.2	20.5	18.8	18.0
5 P.M.	28.5	26.0	26.0	22.0	20.5	18.8	18.0
July 15, 2 P.M.	28.0	28.2	27.0	24.0	20.2	18.7	18.5
3 P.M.	28.0	27.5	27.2	23.7	20.8	18.5	17.7
4 P.M.	28.7	27.2	27.1	22.5	20.2	18.5	17.5
Average	28.2	27.6	27.4	22.7	20.5	18.7	18.1

TABLE II (Continued)

	Ai		Soil				
	5 ft.	6 in.	Surface	1 in.	6 in.	12 in.	18 in.
Sand dune							
July 10, 3 P.M.	29.4	30.8	41.2	36.5	31.0	25.5	24.5
4 P.M.	28.6	30.3	37.5	35.0	30.0	25.7	22.0
5 P.M.	28.9	30.6	36.0	34.5	30.0	26.0	23.0
July 15, 2 P.M.	29.0	30.5	42.5	34.0	29.0	23.0	23.0
3 P.M.	30.5	32.0	46.0	36.0	29.5	26.0	25.2
4 P.M.	31.0	32.0	42.5	34.0	29.0	27.0	25.5
Average	29.6	31.0	41.0	35.0	39.7	25.5	23.9
Basswood-maple forest							
July 22, 5 A.M.	22.0	22.0	21.0	18.0	17.5	16.5	15.5
6 A.M.	22.0	21.5	21.2	18.2	17.2	16.0	15.0
7 A.M.	22.0	21.5	21.3	18.0	17.3	16.0	15.0
8 A.M.	23.5	22.0	23.0	22.0	17.3	16.0	15.0
Tamarack bog							
July 22, 5 A.M.	21.0	20.0	19.0	19.0	17.0	16.0	15.0
6 A.M.	20.5	20.0	19.0	19.0	17.0	16.0	15.0
7 A.M.	22.0	22.0	20.5	19.0	16.5	16.0	15.0
8 A.M.	24.0	23.0	21.5	19.5	17.0	16.0	15.0
Oak forest							
July 22, 5 A.M.	21.1	20.3	19.0	18.8	18.0	17.3	16.2
6 A.M.	21.1	20.3	19.1	18.6	17.7	17.0	16.2
7 A.M.	23.0	22.3	19.2	19.0	18.1	17.2	16.4
8 A.M.	24.4	24.0	21.1	19.1	18.1	17.0	16.8
Pine plantation							
July 22, 5 A.M.	20.0	19.7	19.0	19.2	19.0	—	17.5
6 A.M.	21.0	20.5	19.5	19.5	18.7	18.5	17.5
7 A.M.	21.7	21.7	21.0	20.8	18.8	18.5	17.5
8 A.M.	24.5	24.0	23.0	21.0	18.7	18.5	17.5
Sand dune							
July 22, 5 A.M.	21.8	22.0	23.4	23.0	23.6	24.0	23.0
6 A.M.	23.4	22.6	23.4	23.0	24.0	24.0	23.0
7 A.M.	26.4	27.0	27.4	24.0	24.0	24.0	23.0
8 A.M.	28.3	29.5	32.0	28.0	24.0	24.0	23.0

during the 6 hottest weeks of the year. He has given the limits of the Transition Zone as between the mean temperatures of 64.4° F. and 71.6° F. for the 6 weeks and for the Upper Austral Zone between 71.6° F. and 78.8° F. According to the maps which Merriam has prepared, all of our stations would fall about in the center of the Transition Zone. According to the data which we have collected, it is possible to place the Weather Bureau stations and the sand dunes in the Upper Austral Zone and the rest of the stations would fall within the Transition Zone. This serves to emphasize the fact that life zones cannot be made rigid and that there may be considerable variation within any zone which is made up by using temperature values for its basis.

A COMPARISON OF THE TEMPERATURES IN VARIOUS STRATA OF THE DIFFERENT ENVIRONMENTS

Continuous records of the temperature in different strata of the environments were not available for statistical analysis comparable to that of the regular instrument stations just considered. However, the records taken in the various strata of the different environments are strictly comparable as to

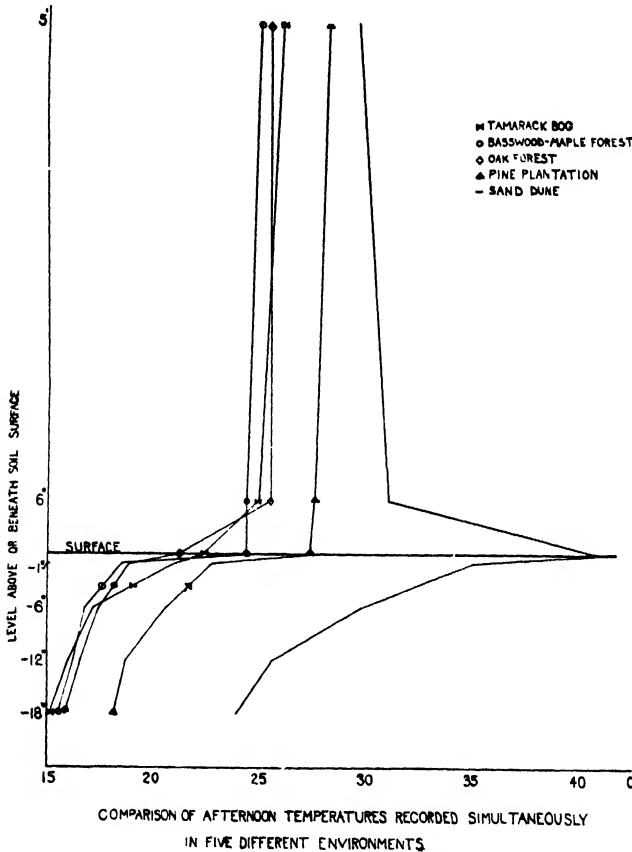


FIG. 6. Comparison of afternoon temperatures recorded simultaneously in 5 different environments.

time, and are very consistent in temperature as shown in Table II and in figures 6 and 7.

Inasmuch as the sand dune has little or no vegetation, its fauna lives on and in the soil stratum, and there are no animals living at the level of the instrument shelter. Consequently the temperatures given by the recording thermometer at this station do not represent the environment occupied by any of the animals. In all of the other environments there were animals living at the level of the thermographs. All of the forest environments are very much

alike in their air and soil temperatures, and differ consistently from the sand-dune temperatures which are considerably higher in all cases. There are certain limited areas between the trees of the young pine forest upon which the sun shone for a long period each day, and in which the soil temperature rose even higher at times than those on the sand dunes. This is due to the shelter from the wind offered by the young trees, and applied only to relatively limited areas. In general, the temperature conditions in the various types of

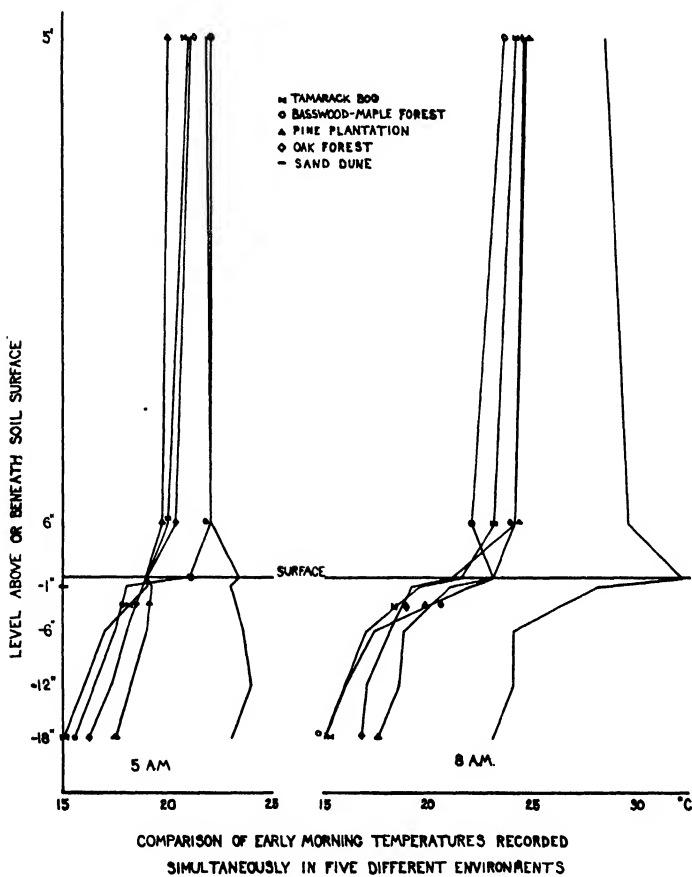


FIG. 7. Comparison of early morning temperatures recorded simultaneously in 5 different environments.

forests were very closely similar and very much like the Weather Bureau stations. Measurements in one day showed a variation of hardly more than 1°C . from the ground surface to 25 feet in various parts of the interior of the tamarack bog. The greatest difference between the sand-dune and the forest environments is at the surface of the soil which happens to be a very important stratum in the sand-dune environment. The temperatures at various depths down to 18 inches show a very consistent difference between the sand-dune

and the other environments. The soil surface temperatures on the dunes may often be from 15 to 25° C. higher than the soil surface in the forests. Even at 5 A.M., when the temperatures in general are at their minima, the soil in the sand dunes is about 5° C. above the other environments. A study of Table II will show that there are not sufficient data available to make distinctions between the soil temperatures of the various types of forest. It seems at present that their soil surface temperatures are about the same, with the possible exception explained for the young pine forest.

SUMMARY AND CONCLUSIONS

A comparison has been made of thermograph records for the 6 hottest weeks of the growing season from the St. Paul and Minneapolis Weather Bureau stations and stations established on the sand dunes, a pine plantation, an oak forest, a basswood-maple forest and a tamarack bog, all of approximately the same altitude and very near the 45th parallel of latitude. Some records of the variation of temperature in different strata of the environments were also made. It has been found that the mean daily temperatures of the different environments are not widely different from those of the Weather Bureau stations, although the 2 forests and the tamarack bog included in the study showed averages over 2° F. less than the Weather Bureau for the period under consideration as contrasted with the station on the sand dunes which was nearly coincident with the bureaus. Incidentally, the difference in mean temperature for the 6 hottest weeks places the Weather Bureaus and the sand dunes in the Upper Austral life zone of Merriam while the forests and the bog fall in the Transitional Zone, which is the zone indicated for the region concerned in Merriam's maps.

The mean daily temperature of the basswood-maple forest, the tamarack bog and the dunes were compared by the use of regression lines. Although there is a high degree of correlation between these 3 pairs of environments, the regression lines showed plainly the tendency of the forest and bog to be cooler than the dunes on warm days but warmer than the open dunes on cool days during the summer. This indicates the effect of the forest in preventing air currents and in intercepting the sun's heat in the crowns as well as in the prevention of reradiation of heat absorbed.

When the mean hourly temperatures for the period are examined it is seen that all of the environments except the sand dunes remain fairly close together during the course of the daily temperature fluctuation. The dunes heat up faster during the fore part of the day and cool more quickly after the sun has passed its zenith than do the other stations. The 2 Weather Bureaus do not deviate far from the all-station mean during the day, but at night they remain significantly above the natural environments. This may be explained by the accumulation of heat in the streets of the city areas where the Bureaus are located.

A study of the temperatures at the various strata of the different environ-

ments shows that the forests are very nearly alike in all their strata and that the sand dunes range from 5° to 20° C. higher at the soil surface. This is considered very significant in that the soil stratum is the only one normally available as an animal habitat on the sand dunes. Even at a depth of 18 inches the sand dune is consistently 5° C. or more warmer than the soil of the other environments during the hottest part of the year.

It is concluded that for the 6 week summer period the records of the Weather Bureau stations in either St. Paul or Minneapolis give a fair index of the air temperatures for the immediate climatic area. However, if the mean temperature of a given environment for a shorter period is considered, the Weather Bureau record is liable to be a less accurate index. Furthermore if nocturnal temperatures only are considered the Bureau records are found to be somewhat above the actual temperatures in the natural environments.

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MOUNTAIN LAUREL AND RHODODENDRON AS FOODS FOR THE WHITE TAILED DEER

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The forests of Pennsylvania support an enormous herd of deer, which constitute a charming feature of the out-of-door life of the state, and also furnish sport for an army of hunters.

These deer, however, have become so numerous that they cause serious damage to field crops and orchards; and, since they mingle freely with cattle and sheep, and are capable of carrying the diseases of these animals, they constitute a definite menace to the livestock industry of the state. So numerous, in fact, have the deer become in certain regions that the forest has been cleared of every edible leaf and twig to a height as great as the deer can reach, thus forming a clear-cut "deer line" in the vegetation; and large numbers of deer have died in these overstocked forests in the early spring during several recent years.

This situation is a matter for concern not only in relation to the well-being of the deer of the state, but also as it affects the sanitation of watersheds.

The Pennsylvania State Board of Game Commissioners, therefore, felt a need for full information as to the cause of the death of these deer, for its own guidance in the administration of the game law, and for the information of the people of the state, especially in order that hunters may be able intelligently to support the law. Accordingly the Board of Game Commissioners requested the Pennsylvania State College to determine, if possible, the cause of the death of the deer in the forests during the early spring, and especially to determine whether mountain laurel (*Kalmia latifolia*) and rhododendron (*Rhododendron maximum*) are poisonous to deer.

The stomachs of the dead deer are very commonly found to contain the leaves of laurel and rhododendron in quantity, and these plants have been known to be poisonous to cattle, sheep, and human beings for many hundreds of years, at least since the days of Xenophon and Pliny, both of whom knew of their poisonous character.¹

Inquiry among those who are in best position to know about the matter failed to bring to light information directing especial suspicion toward any other plant as the cause of the death of the deer. This phase of the problem, therefore, involved only the consideration of these two plants.

¹ The most satisfactory review in English of the knowledge of the poisonous principle of the laurels (rhododendron is a laurel) is by S. W. Hardikar, "On Rhododendron Poisoning," *Jour. Pharmacol. and, Exper. Therapeutics*, 20: 17-44, 1922.

An experimental study was therefore conducted at the College, in co-operation between the Board of Game Commissioners, the Institute of Animal Nutrition, and the Agricultural Experiment Station.

A feeding plant for this study was constructed on the College farm. About 4 acres of woodlot were inclosed, and divided into 5 long, narrow lots and a larger nearly square "pasture," by means of 8-ft. wire fence. A shelter shack was built for the storage of feed; and a small open shed was built in each experimental pen, to serve as shelter for the deer in stormy weather. The deer made almost no use of these shelter sheds, however, and even in cold and snowy weather preferred to lie out in the open.

During the summer of 1929, the game protectors of the state picked up the orphan fawns which came to their attention, and raised them on cow's milk for this study. As these fawns reached the weaning age, in the fall, 22 of them, and a yearling buck, were brought to the College, and became the subjects of this investigation.

In order that the fawns should have no feed but that which was provided by the experimental program, all available browse was removed from the small feed lots in which the deer were confined, though an abundance of trees remained for shade, and the brush in the large lot, which lay to the northwest of the smaller feed lots served as an effective windbreak.

After the arrival of the fawns at the College they were given milk for a few days only, and then, after a little "cutting and trying" to find out what they would eat, they were put onto a ration of equal parts of whole corn, whole oats, and pea-size linseed oil cake, with alfalfa hay for roughage. This proved to be an entirely satisfactory ration, and was used as a standard treatment at all times except when the fawns were on special experimental feed. No difficulty was experienced in feeding the fawns, and not one was ever sick while eating this standard mixture. They took to the grain ration without hesitation, and also liked the alfalfa. Their eating of this hay was very wasteful, however, because they carefully picked off the leaves, and never ate the stems. They would not eat appreciable quantities of either timothy or clover hay.

EXPERIMENTAL TREATMENT

On November 14, two of the fawns were shut up, one in each of two of the small shelter sheds. After fasting them for 24 hours one was given laurel and the other rhododendron for $5\frac{1}{2}$ days.

On account of the confinement of the deer and separation from their fellows, both were exceedingly restless, and ate very little of the feeds of interest. They preferred to eat leaf mold from the ground, dead oak leaves, and woody branches rather than leaves of laurel and rhododendron.

In both cases the deer showed aversion for the laurel and rhododendron leaves, and at the end of $5\frac{1}{2}$ days were eating much less of them than at the beginning.

If either the laurel or the rhododendron was offered to a deer he would accept it, take a nibble, and then drop it, never eating it entirely, and obviously not at all attracted to it. The average daily consumption of these feeds was in each case about 6 ounces of the fresh material per head per day (168 grams of the laurel, and 173 grams of the rhododendron). These quantities were equivalent to a very small fraction of a maintenance ration. No unfavorable effects were observed from the eating of these plants.

Between November 20 and 25 (5½ days), 9 deer were given laurel and 9 others were given rhododendron along with their customary grain ration, with the free run of the feed lots as usual.

The deer receiving laurel ate an average of 38 grams (1.3 oz.), and those receiving rhododendron ate 61 grams (2.2 oz.) per head per day.

In other words, if the deer could eat grain they ate almost none of the plants of interest.

On November 22, a wild deer which had been injured by being caught in a wire fence in the Seven Mountains region was brought into State College, and was killed by a game protector to end its suffering. Its stomach was found to contain laurel and rhododendron alone.

Between November 26 and December 2, three deer were confined in each of two shelter sheds, one lot receiving laurel alone and the other rhododendron alone for the 6 days.

These deer ate much more of the plants of interest than did those previously confined singly, those receiving laurel eating 478 grams (16.9 oz.) and those receiving rhododendron 558 grams (19.7 oz.) per head per day. No unfavorable effect was noted. These fawns averaged about 50 pounds each in weight.

An effort was then made to learn how much laurel and rhododendron the deer would eat if they were given these feeds with grain during an extended interval of time, the idea being that under these conditions a developing sense of need of roughage might induce them to eat larger quantities.

Two lots of fawns, 8 in each lot, therefore, were given laurel and rhododendron, respectively, with grain, but with no hay, from December 20 until February 13, a total of 49 days.

The animals seemed contented but lived mostly on grain, and ate very little of the feeds of interest. The conditions of weather, etc., were such that significant weights of the laurel and rhododendron consumed could not be determined. They ate about half as much again of the laurel as of the rhododendron, and ate more of both in cold than in mild weather.

During this time the fawns ate about 700 grams (1.5 pounds) of grain per head per day. They shivered in severe weather, but still preferred to be in the open rather than under the sheds provided.

On January 27 one fawn receiving rhododendron seemed out of condition. It staggered slightly as it walked, and its eyes looked dull. This appearance passed off, however, and did not recur during the later feeding of rhodo-

dendron alone. Otherwise no unfavorable effects of the treatment were noted.

On February 13 it was determined to make a long-time test of laurel and rhododendron alone. The grain, therefore, was taken away from the fawns at once; and one lot of 8 was given laurel and the other rhododendron (Fig. 1).

After the withdrawal of the grain the fawns reversed their preference for



FIG. 1. Yearling deer subsisting on laurel and rhododendron alone. A pile of branches from which the leaves have been eaten is shown at the left.

the two feeds of interest, and began eating much more rhododendron than laurel.

On February 20 the lot which had been receiving laurel alone was given laurel and rhododendron, and thereafter ate mostly the latter, but continued to eat some of the laurel.

The two lots of deer were then continued on the two treatments specified until March 29, making in all 45 days for one lot on rhododendron alone, and for the other lot 7 days on laurel and 38 days on laurel and rhododendron. No unfavorable effects were noted.

During the last two tests the 16 fawns in the two experimental lots received laurel, or rhododendron, or both, every day for 94 days; and during this period received no other roughage of any sort, except that they did gnaw the bark from a few little wild cherry trees growing in their feed lots.

During the last 45 days, during which the fawns received laurel and rhododendron alone, and no grain, they became very thin and weak, and it was

perfectly obvious that they were not eating enough of these feeds to maintain their weight. In order to have definite figures to confirm this observation the two lots of fawns were each weighed at the same time of day on March 20 and again on March 29.

During these 9 days the fawns which received laurel and rhododendron decreased in average weight from 59.1 pounds to 56 pounds, while the deer which received rhododendron alone decreased in weight from 52 to 49.75 pounds.

There was no appearance of poisoning, but the deer had reached a very low state of vitality and of spirit. They acted more like undernourished calves than like deer, and in both of the experimental lots there was enlargement of the ends of the long bones of the legs—apparently incipient rickets.

On March 29 the experimental treatment was discontinued, and the deer were restored to the stock ration of corn, oats, linseed oil cake, and alfalfa hay, with an additional allowance of mangel-wurzels. Also, they were given the freedom of the large lot, in which they had access to normal browse. The improvement in the behavior of the deer was marked and immediate, and within a few weeks they returned to normal condition, except that indications of rickets persisted.

In order to determine the character of laurel and rhododendron as feeding stuffs, ordinary feed analyses were performed on rhododendron leaf, rhododendron bud, and laurel leaf, bud, and green stem—as eaten, for the purpose of comparison with analyses of farm feeds of known character and of similar composition. The results are given in Table I.

In such a crude analysis there is no indication of the lack of palatability of laurel and rhododendron, and of their unsatisfactory nutritive character. In fact, mountain laurel, as eaten, seems in the light of this analysis, to have a composition about like that of ripe timothy.

TABLE I. *Analyses of rhododendron and mountain laurel in comparison with analyses of feeds of known character and of similar composition*

Substance	Water	Ash	Crude protein	Carbohydrate		Fat
				Fiber	N-free extract	
Rhododendron leaf	44.35	1.77	2.34	9.21	40.08	2.25
Rhododendron bud	38.89	1.22	2.04	9.66	46.18	2.01
Mountain laurel leaf, bud, and green stem	53.99	1.94	4.24	7.93	29.09	2.81
Timothy, in seed	53.60	2.30	3.1	15.3	24.4	1.3
Corn husks	24.70	2.50	2.9	24.9	44.2	0.8
Corn stover, high in water	41.0	3.80	3.9	20.1	30.2	1.0

Points worthy of note in the method of the deer in eating laurel and rhododendron are that it is customary for them to eat the laurel more completely than the rhododendron; thus, in eating laurel a deer usually eats not

only the leaves, but also the green stems of the preceding season's growth, and some of the ripe wood; while in eating rhododendron the bud is the preferred part, the leaves often being cut off and allowed to fall to the ground,—the deer eating only the buds and the green twigs.

Since the deer exercise a marked selective capacity in eating these plants, it is not easy to collect samples exactly representative of the feeds as eaten.

In order to supplement the experimental findings with observations on the feeding habits of the deer in the forests of the state, a request was made of the Board of Game Commissioners that game protectors report the contents of the stomachs of the deer which they had occasion to examine during the hunting season. This request was transmitted to the game protectors, but few reports were received. A condensed statement of these observations, as submitted by Dr. Thos. E. Winecoff, in charge of research for the Board of Game Commissioners, is as follows:

Cumberland County. Fifteen deer were examined and all found to have been feeding on grasses, rhododendron, laurel, and the young sprouts of various species of local forest growth.

Tioga County. Forty-four deer were examined. One was found to have been feeding on laurel, wintergreen, and sumac seeds; one on wintergreen, sumac twigs, and sumac seeds; one on sumac seeds, twigs, burdock, and dry birch leaves; one almost exclusively on laurel; and 21 had been feeding on dry birch leaves and wintergreen. In 15 deer the stomach contents were too far digested for positive identification.

Susquehanna County. Four deer were reported on; 2 with stomachs containing about 60 per cent grass of various species and 40 per cent apples; one 75 per cent grass and 25 per cent apples, and one with half-and-half grass and apples.

Four deer were reported on from a county not named, all having been feeding on laurel and wintergreen.

Perry County. The stomach of one deer contained corn, corn fodder, sumac buds, and green clover.

These reports simply reflect the great diversity of the products, including laurel and rhododendron, which are eaten by deer.

Late in April there was an interval of 4 days—the 23d to the 26th—during which the weather was stormy and unseasonably cold, reaching minimum temperatures of 23° F. and 22° F. on the 23d and 24th, respectively. During this time the deer, which were in a low state of nutrition as a result of the previous confinement to laurel and rhododendron, suffered much from the cold, and one died from pneumonia. A letter received at this time from I. H. Bartlett, of the Michigan Game Division, seems to lend point to the above observation by reporting that veterinarians and other investigators of the deer yarding problem in Michigan had attributed cases of death of deer to pneumonia.

Also, late in April, one of the deer which seemed to be suffering from

rickets was killed, and photographs are presented of the hind feet (Fig. 2), showing enlargement at the fetlock joint, and cross sections, sawed in two directions, of the metacarpus (Fig. 3).

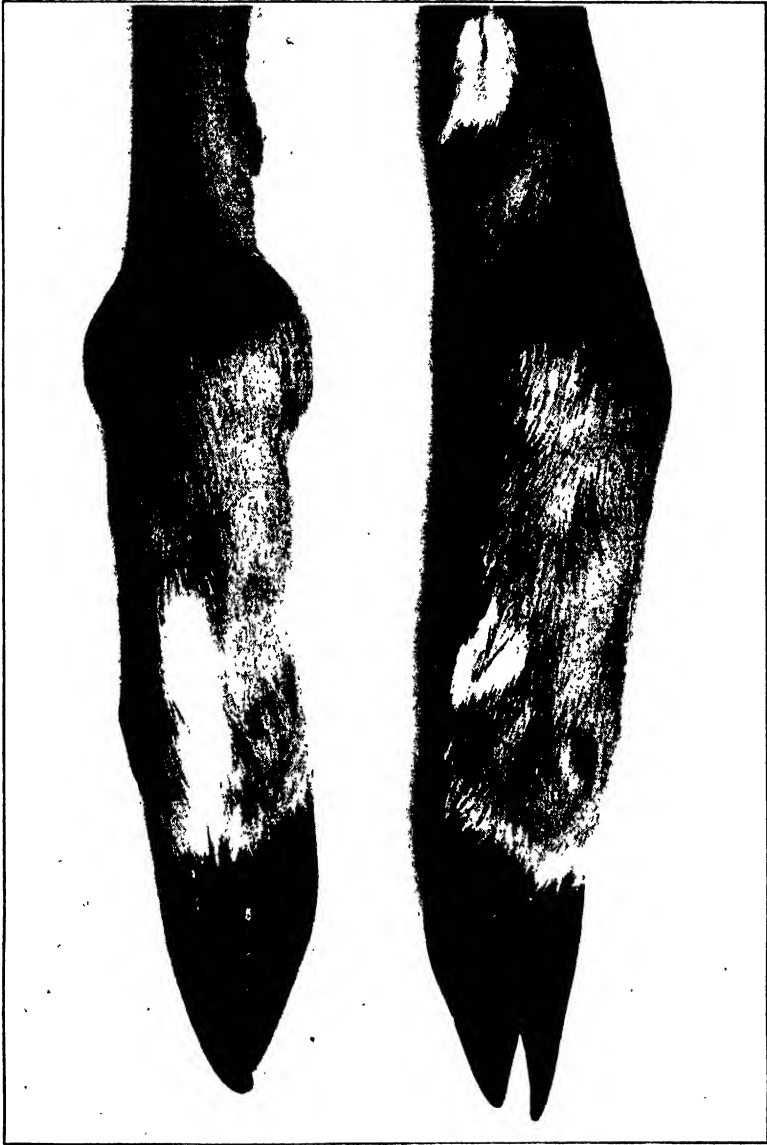


FIG. 2. Hind feet of yearling deer, affected with rachitis.

Superficial indications were borne out by the conditions revealed by the sectioning of the bones, and there is no question but that this deer was suffering from an early stage of rachitis.

Slight enlargement of the distal ends of the ribs was noted, and the ribs were so brittle that they could be broken with the fingers with great ease; lymph glands were hemorrhagic, and petechiae of the tissues in general were conspicuous.

In order to extend this observation to the practical conditions of interest

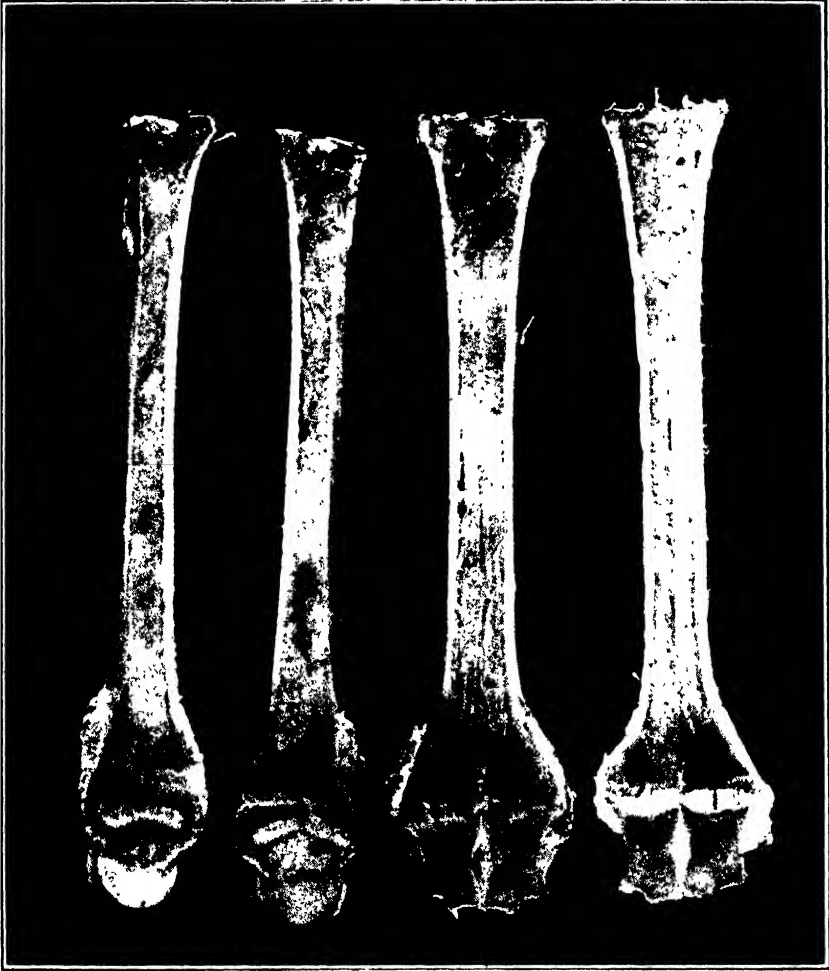


FIG. 3. Metacarpal bone of yearling deer, affected with rickets.

in the state, the Game Commission had sent to this Institute, for examination, the canon bones of 4 fawns which were found dead in the forest by John Lohmann, Game Protector, in Pike County.

In one case the bones were normal; in another the organic substance was too much decomposed for satisfactory examination; in another there was slight evidence of rickets; and in the fourth case there was moderate but unmistakable evidence of rickets.

Having definitely shown that deer are not visibly injured by the eating of laurel and rhododendron, even when forced to subsist on these plants alone, there remained the academic question as to whether deer can be killed by the force-feeding of these plants in larger quantities than are voluntarily eaten.

To determine this point a quantity of each of the plants was dried in an electrically heated air oven at a temperature of 60° C. (140° F.), and were then finely ground in a sample mill, as for chemical analysis.

As a means of administering these dried and ground leaves the authors adopted a painter's calking gun, and mixed the dried and ground leaves with a sufficient proportion of cooked or uncooked flour paste so that it could be forced from the instrument. The nozzle of the gun was extended 4 inches by the use of a rubber tube with an internal diameter of 5/16 inch, by means of which the dose was placed in the back of the mouth of the deer, from



FIG. 4. Force-feeding a yearling deer, to determine tolerance for laurel and rhododendron.

which position the deer could not spit it out. This process is illustrated in figure 4.

On April 29, after a preliminary fast of 24 hours, a fawn weighing 90 pounds was fed laurel leaf equivalent to 1.75 per cent (fresh basis) of the live weight; result, death.

On May 1 a fawn weighing 82 pounds, after a 24-hour fast, was fed laurel leaf equivalent to 1.29 per cent (fresh basis) of the live weight; result, after 4½ hours, nausea, irregular respiration, much distress, and incoordination of movements, respiration rate 18 per minute; during the next 3 hours the pathologic symptoms increased in severity—the animal *in extremis*; 2 hours and 45 minutes later the fawn had improved in condition, pulse rate 40, respiration 35; regained normal condition within a few hours. The quantity of laurel fed was apparently about at the limit of toleration.

On May 8, after a fast of 24 hours, a fawn weighing 70 pounds was fed rhododendron leaf equivalent to 1.72 per cent (fresh basis) of the live weight. This quantity seemed to be as much as it could swallow. Two hours and a quarter thereafter the deer may have manifested slight nausea, but was alert and not definitely abnormal in any way, and no pathological symptoms appeared later.

On the same day another deer, weighing 58 pounds, was force-fed 300 grams of oat feed, and 450 grams of wheat flour, plus water, at one time, in order to test the effect of the process of force-feeding on the animal. There was no unfavorable effect of any sort.

On May 29, a fawn weighing 74 pounds, after a 36-hour fast, was force-fed green rhododendron leaf equivalent to 2.25 per cent of the live weight; and a second fawn, similarly fasted, and weighing 57 pounds, was force-fed green rhododendron leaf equivalent to 1.35 per cent of the live weight. In both cases the ground leaf was mixed with raw flour and water, to produce the consistency required; but in neither case was there any indication of poisoning or of other unfavorable effect of any kind.

CONCLUSION

In the light of the results of these experiments, supplemented by other published observations made by or for the Board of Game Commissioners, the usual chain of causes of the death of fawns in the forests of the state seems to begin with the disturbance of the normal ratio of males to females, among the deer, as a result of the greater protection which has been given the females by the law regulating the hunting of deer; this unbalancing of the sexes having the effect of delaying conception by many does—their young being born late, and coming into the winter too small to compete for food, on favorable terms, with larger deer. These late fawns, therefore, are restricted, in seasons and in regions of feed shortage, to the less palatable and less nutritious feeds, especially to laurel and rhododendron; and under these conditions many have died, apparently as a result of undernutrition, cold, pneumonia, and rickets.

SUMMARY

Mountain laurel (*Kalmia latifolia*) and rhododendron (*Rhododendron maximum*) are eaten with considerable freedom by deer, especially in times

of feed shortage; but as thus eaten seem not to be poisonous, as they are to cattle and to sheep.

Young deer, approaching one year of age, when held in confinement, showed that they did not like laurel and rhododendron, and if allowed grain in addition would eat very little of these plants.

When restricted to laurel or rhododendron alone (without grain) the young deer would not eat enough of either plant to maintain the live weight.

Young deer were restricted to laurel or rhododendron and grain for 49 days. They remained contented and in good health. Then the grain was withdrawn, and the deer continued on laurel and rhododendron alone for 45 days. During this interval the deer became very thin and weak; they suffered from the cold, and one died from pneumonia; they also developed a mild condition of rickets, but did not exhibit symptoms of poisoning by the toxic principle of the laurel and rhododendron. Some evidence of rickets was also present in fawns found dead in the forest.

In the force-feeding of laurel leaf a deer was just able to tolerate and to recover from the effects of this plant in a quantity equal to 1.29 per cent of its live weight; another deer being killed by the force-feeding of 1.75 per cent of its live weight of laurel leaf.

The toxic principle of laurel and rhododendron, therefore, is poisonous to deer, though they seem not to eat, of their free will, enough of either of these plants to exceed their tolerance for them.

Three deer were force-fed 1.35 per cent, 1.72 per cent, and 2.25 per cent, respectively, of rhododendron leaf, but in no case was there definite pathologic effect; rhododendron, therefore, seems to be less toxic than laurel.

These experiments and other published observations indicate that the cause of death of the fawns in the forest begins with the disturbance of the normal sex ratio. The excess of females results in delaying conception by many does, so that the late fawns, too small to compete with the larger deer, are restricted, in times of shortage, to less suitable feeds, and many have died, apparently from undernutrition, cold, pneumonia and rickets.

The writers wish to express their grateful indebtedness to Mr. John J. Slautterback, Executive Secretary of the Board of Game Commissioners, to Dr. Thomas E. Winecoff, who is in charge of the research work of this Board, to Mr. John B. Ross, Division Game Supervisor, and to Mr. Thos. A. Mosier, District Game Protector, for their generous support, advice and assistance in the conduct of this study; to Dr. C. Dwight Marsh, Associate Physiologist in the U. S. Bureau of Animal Industry, for suggesting the force-feeding of the deer, and the dosage employed, to Dr. J. F. Shigley and to Associate Professor P. S. Williams for assistance in the force-feeding, and to Mr. John H. Smith for faithfully performing the principal part of the labor involved in this study.

GEOGRAPHICAL DISTRIBUTION OF VARIABILITY IN THE YIELDS OF CEREAL CROPS IN SOUTH DAKOTA

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In a recent paper (Klages, '30) the difference in the degrees of variability in the yields of various field crops for the states of the Mississippi valley were discussed. It was found that the seasonal fluctuations in the yields of all crops, except wheat in the states producing hard red winter wheat, were greater in the Great Plains states than in the more humid states to the east. Marked differences were also pointed out in the trends of the yields of these crops over a 37 year period, as well as in the degrees of correlation existing between the yields of separate crops of the respective states in the two sections. The data presented indicated that the geographical localization of the lowest degrees of variability in the seasonal yields of a crop, or a series of crops, corresponds well to the section to which that particular crop or group of crops is best adapted.

The facts brought out in the investigation referred to above have general application only. The specific effects of climatic factors are, as is commonly known, modified to a considerable extent by other factors of the environment, especially by variations in local soil conditions. Furthermore, the climatic conditions of as large an area as the confines of a state are far from uniform. This is especially true for the Great Plains states, with their eastern portions in a type of climate entirely different from that of their central and western parts. As may be observed from the maps of natural vegetations given by Shantz and Zon ('24), and from the various root studies of native plants by Weaver ('20) and by Weaver and Crist ('22), entirely different types of vegetation, which reflect directly the prevailing climatic conditions, are encountered in the eastern and western portions of these states. Consequently the values given on yields, variability of yields, etc., of such large units have all the shortcomings of average values. The justification for the employment of such large units as the areas of individual states was found in that they offered the only available source of information. With these points in mind it was thought worth while to take up the study for the confines of one state only, and in that state from only well defined locations.

The distribution of the main station and the various sub-stations of the South Dakota Agricultural Experiment Station was found favorable for a more definite, and in some respects a more detailed, investigation on variability of crop yields. Figure 1 shows the distribution of these stations over the state. The main station at Brookings is located in the east-central part

of the state, only 18 miles from the Minnesota line. The Highmore sub-station is located in the central part, 155 miles west of Brookings, while the Eureka sub-station is found 100 miles almost due north of Highmore, near the North Dakota state line. Results were taken only from the above three mentioned stations. Continuous yield records for a long enough period of time for statistical analysis were not available at either the Vivian or the

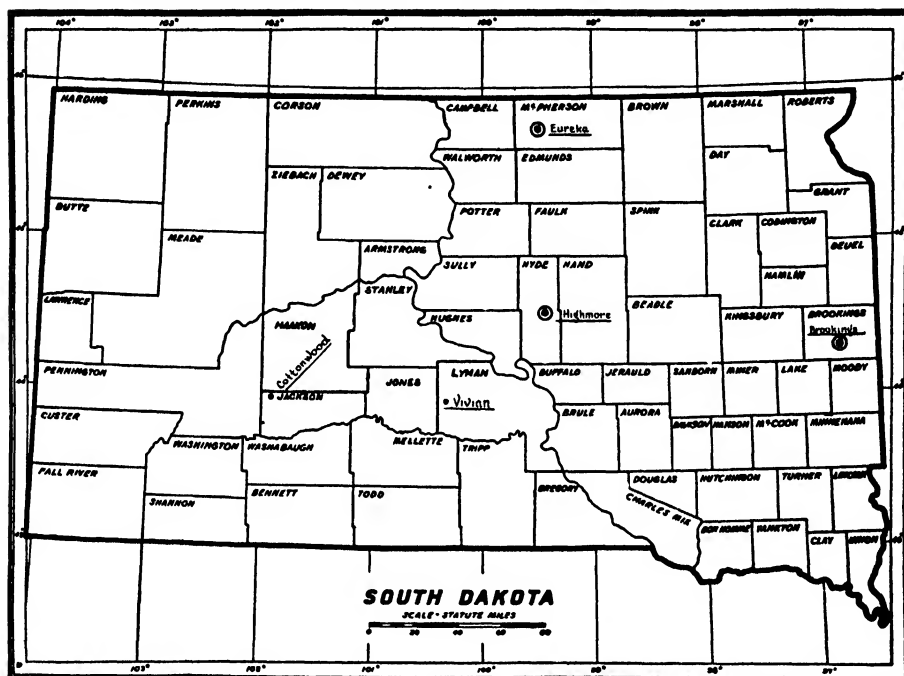


FIG. 1. Location of the main and sub-stations of the South Dakota Agricultural Experiment Station.

Cottonwood sub-stations located in the south-central and western parts of the state.

The yields of the various cereal crops to be discussed were taken from the variety test plats at Brookings, Highmore and Eureka. Yields of the same standard varieties were available from the Brookings and Highmore test plats for a 25 year period (1905-1929) while comparable yields from the plats at Eureka were available for only a 21 year period, from 1909 to 1929 inclusive.

AVERAGE YIELDS AND VARIABILITY IN THE YIELDS OF CEREALS AT BROOKINGS, HIGHMORE AND EUREKA

Since continuous, comparative variety tests have been conducted for a longer period of time at Brookings and Highmore than at Eureka, it is necessary to present the data on average yields and seasonal variability of such

yields in two separate tables. Table I gives these data for the first two stations for a 25 year period, while Table II gives the same data for all three stations for a 21 year period. All crops listed in the tables, with the exception of Turkey 144, a winter wheat, were grown for the years indicated. Yields of Turkey 144 were available for only a 23 year period. Winter wheat was not grown at Highmore in 1909 and 1910 or at Brookings in 1910 and 1911.

It was necessary in certain instances to make use of the yields of two or

TABLE I. *Average yields and degrees of variability of the yields of cereal crops grown on variety test plats at Brookings and Highmore, South Dakota, for a 25 year period, 1905-1929*

Crops and varieties	Brookings		Highmore	
	Average yield in bu. per acre	Coefficient of variability of yields	Average yield in bu. per acre	Coefficient of variability in yields
Wheat				
Winter, Turkey 144.....	25.2±1.64	48.45±5.61	13.8±2.05	110.13±19.44
Durum, Kubanka.....	17.0±1.20	52.12±6.17	15.8±1.33	62.45±7.95
Common Spring ¹	15.6±1.06	50.71±5.95	12.9±1.09	62.88±8.03
Oats				
Early, Sixty Day.....	54.8±2.77	37.48±4.05	43.2±3.81	65.45±8.51
Late, Swedish Select.....	44.7±2.94	48.68±5.64	34.4±3.40	73.20±10.05
Barley				
Six rowed, Odessa.....	44.1±2.38	40.06±4.39	31.1±2.66	63.30±8.10
Two rowed ²	34.5±2.22	47.33±5.43	27.1±2.12	58.03±7.16

¹ Brookings, Preston 1905-1912, Marquis 1913-1929; Highmore, Preston 1905-1929.

² Brookings, Chevalier 1905-1912, White Smyrna 1913-1929; Highmore, White Smyrna 1905-1929.

more varieties of some of the groups of crops as indicated in the footnotes of the tables. Where this had to be done in order to secure continuity of data, precautions were taken to select varieties with similar habits of growth. Thus, since White Smyrna barley was not included in the variety test plats at Eureka, the yields of Hannchen, a two-rowed barley with a growing habit similar to that of White Smyrna were substituted for it.

As may be seen from Tables I and II, and from figure 2, the yields of all crops were higher at Brookings than at the two stations to the west. This is to be expected in view of the greater amounts of precipitation in the eastern than in the central parts of the state. The average annual rainfall over a period of 21 years, 1909-1929, at Brookings was 19.91 inches as compared to 17.35 and 15.99 inches respectively for Highmore and Eureka over the same period. Data on the rates of evaporation during the growing season for the different stations are not available; but it is known that, due to the higher summer temperatures and greater wind velocities, the rates are greater in the central than in the eastern portion of the state.

VARIABILITY IN YIELDS OF CEREAL CROPS

April, 1931

TABLE II. *Average yields and degrees of variability of the yields of cereal crops grown on variety test plats at Brookings, Highmore, and Eureka, South Dakota, for a 21 year period, 1909-1929*

Crops and varieties	Brookings		Highmore		Eureka	
	Average yield in bu. per acre	Coefficient of variability of yields	Average yield in bu. per acre	Coefficient of variability of yields	Average yield in bu. per acre	Coefficient of variability of yields
Wheat						
Durum Kubanka.....	16.7 ± 1.37	55.86 ± 7.39	14.0 ± 1.35	69.57 ± 10.16	14.9 ± 1.64	74.95 ± 11.37
Common Spring ¹	15.4 ± 1.17	54.69 ± 7.20	11.7 ± 1.31	75.81 ± 11.57	10.0 ± 1.13	76.81 ± 11.81
Oats						
Early Sixty Day.....	54.5 ± 3.04	37.89 ± 4.48	42.5 ± 4.47	71.46 ± 10.58	36.5 ± 3.67	68.30 ± 9.89
Late Swedish Select.....	45.9 ± 3.33	49.26 ± 6.25	32.3 ± 3.85	80.89 ± 12.79	34.3 ± 3.86	76.4 ± 11.70
Barley						
Six rowed, Odessa ²	45.1 ± 2.74	41.19 ± 4.96	30.5 ± 3.12	69.38 ± 10.12	21.5 ± 2.55	80.26 ± 12.66
Two rowed ³	33.3 ± 2.22	47.94 ± 6.03	26.3 ± 2.44	62.99 ± 8.78	23.2 ± 2.47	72.22 ± 10.75
Flax ⁴			7.0 ± .94	97.55 ± 17.30		

¹ Brookings, Preston 1909-1912, Marquis 1913-1929; Highmore and Eureka, Preston 1909-1929.² At Eureka, Manchuria 1909-1924, Odessa 1925-1929.³ Brookings, Chevalier 1909-1912, White Smyrna 1912-1929; Highmore, White Smyrna 1909-1929; Eureka, Hammen 1909-1929.⁴ Yield for 1909 estimated. Varieties used were, Russian 1910-1911, N. Dak. Resistant 52 1912-1913, N. Dak. Resistant 114 1914-1929.

Tables I and II and figure 3 show very definitely that the seasonal variability in the yields of the various crops considered, as expressed by the coefficient of variability, is decidedly less at Brookings than at the two stations in

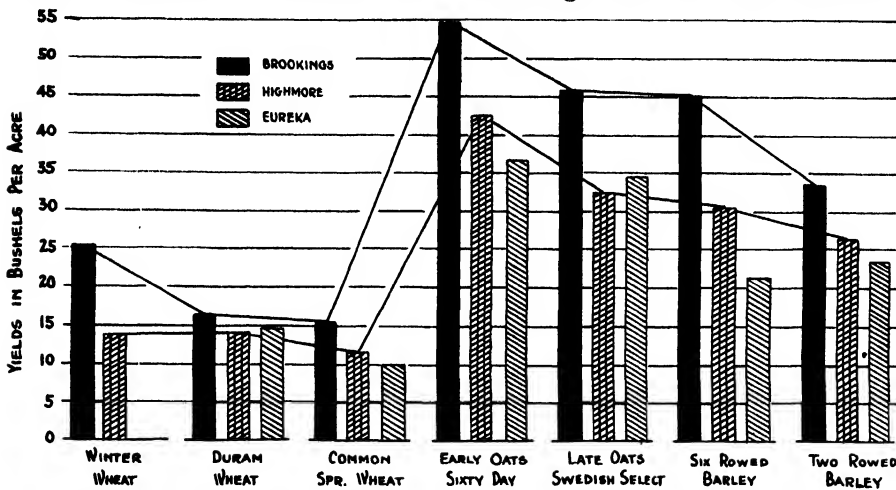


FIG. 2. Yields of cereal crops grown on variety test plats at Brookings, Highmore, and Eureka for a 21 year period, 1909-1929.

the central portion of the state. This substantiates the conclusions in the previous paper (Klages, '30).

Winter ('29) points out that Weinberg's formula (Weinberg, '26).

$$W = \frac{\sigma \sqrt{M_n - M_o}}{\sqrt{(M_a - M_o)(M_n - M_a)}}$$

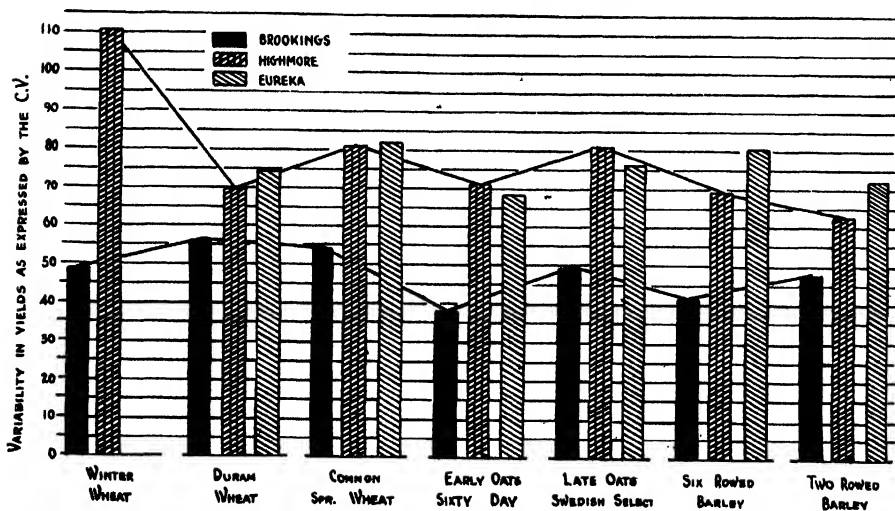


FIG. 3. Variability in the yields of cereal crops grown on variety test plats at Brookings, Highmore, and Eureka for a 21 year period, 1909-1929.

for comparative purposes may give a better conception of variability than does the commonly used coefficient of variability. In this formula W = the coefficient, M_n the highest value in the distribution, M_o the lowest value in the

TABLE III. *Degrees of variability in the yields of cereal crops grown on variety test plats at Brookings, Highmore, and Eureka, South Dakota, for a 21 year period, 1909-1929, as expressed by Weinberg's coefficient*

Crops and varieties	Brookings	Highmore	Eureka
Wheat.....			
Winter, Turkey 144 ¹	3.70	4.92	—
Durum, Kubanka.....	3.24	3.42	3.56
Common spring ²	3.27	4.37	3.22
Oats.....			
Early, Sixty Day.....	4.45	5.70	5.05
Late, Swedish Select.....	4.80	5.93	5.61
Barley.....			
Six rowed, Odessa ³	4.39	4.90	4.66
Two rowed ⁴	4.29	4.25	4.31

¹ 1905-1929 with the exception of two years, Highmore 1909 and 1910, Brookings 1910 and 1911.

² Brookings, Preston 1909-1912, Marquis 1913-1929; Highmore and Eureka, Preston 1909-1929.

³ At Eureka, Manchuria 1909-1924, Odessa 1925-1929.

⁴ Brookings, Chevalier 1909-1912, White Smyrna 1912-1929; Highmore, White Smyrna 1909-1929; Eureka, Hannchen 1909-1929.

distribution, and M_a the mean value of all variants. Table III gives the degrees of variability of the various crops considered at the three stations as expressed by Weinberg's formula. The general deductions to be drawn from the table are like those derived from previous tabulations presented. There are, however, two instances in which the degrees of variability as expressed by the Pearson coefficient of variability and by Weinberg's coefficient fail to agree: namely, in the values for the common spring wheat of Eureka when compared with the figures at the other two stations, and for the values shown for the variations in the yields of the two-rowed barleys at all three stations. The values of Weinberg's coefficient for common spring wheat at Brookings and Highmore show pronounced differences, while the one calculated for Eureka is unduly low in comparison with its high coefficients of variability. The values of the coefficients of variability for the three stations are 54.69, 75.81, and 76.81, while the values of Weinberg's coefficient are 3.27, 4.37, and 3.22 for Brookings, Highmore, and Eureka respectively. Since Weinberg's formula was developed for the measurement of variability of relatively large populations, for a larger number of variants, than used in this investigation, a great deal of significance should not be attached to the two instances of lack of agreement in the values of Weinberg's coefficient and

the coefficient of variability. More will be said later regarding the relative fluctuations in the yield of the two-rowed barleys at the three stations.

YIELDS AND VARIABILITY IN THE YIELDS OF WHEAT

The yields of three different classes of wheat were taken into consideration: namely, those of hard red winter (Turkey 144), hard red spring (Preston and Marquis), and durum (Kubanka).

The smallest differences in the yields of any of the crops used in this investigation at the three respective stations are those for durum wheat. The same is true for the differences in the degrees of variability of seasonal yields at the several stations. Since the differences in the yields of Kubanka at the several stations are not as great as three times their probable errors, they are not statistically of significance. The relatively small differences in the yields, and the smaller differences in the variability of such yields in comparison with those shown by other crops considered in the eastern and central portion of the state, may be explained by the well recognized fact that the

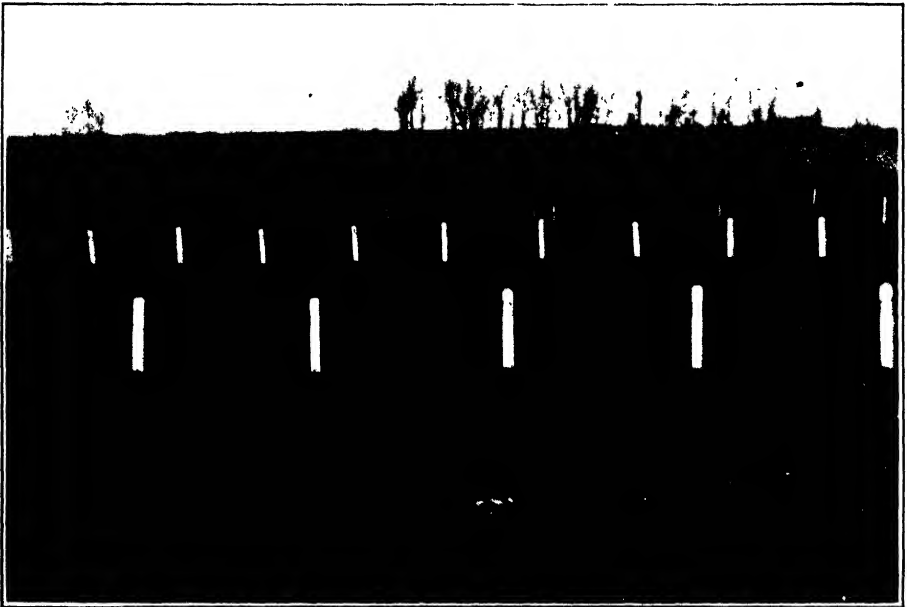


FIG. 4. Winter wheat nursery at Brookings during early January, showing complete absence of cover.

durum wheats (*Triticum durum*) are more drought resistant than the common bread wheats (*T. vulgare*). The common spring wheat yields less than the durum wheat at all stations, the differences in the yields of these two classes for a 21 year period, 1909-1929, being 1.3, 2.3, and 4.9 bushels per acre at Brookings, Highmore, and Eureka respectively. Except at Brook-

ings, where the two values are almost identical, the degrees of variability of the yields of the common wheats are greater than those shown for the durums.

Winter wheat was grown at only two stations, Brookings and Highmore. The differences in the yields and variability of such yields are very pronounced. These differences are due primarily to a greater amount of winter-killing in the central than in the eastern part of the state. Over a 23 year period, 8 complete failures due to winter-killing are on record for Highmore as compared to only one for Brookings during the same period. Winter wheat in the northern Great Plains area is exposed to extreme conditions. Fields are frequently without protection of any kind during cold dry periods. Figure 4 shows the winter wheat nursery at Brookings during severe weather early in January. The complete absence of cover shown is a common occurrence, and more so in the central than in the eastern portion of the state where there is less snowfall and a greater wind velocity to sweep fields clean of snow covers. As a result of these conditions practically no winter wheat is grown in the north-central portion of South Dakota. Even in the eastern part of the state it is best to grow the crop under protected conditions, such as in standing corn stalks which serve to break the velocity of the wind and help to hold snow covers.

YIELDS AND VARIABILITY IN THE YIELDS OF OATS

The yields and variability of yields of oats follow the same general trend as pointed out for wheat. Yields in the eastern part of the state are higher, while the variability of such yields is lower there than in the western portion.

Attention is called to the relative performance of early and later maturing varieties of oats. It is evident from the higher average yields and the lower variability of such yields that early varieties of the Sixty Day type are better adapted to prevailing climatic conditions than later maturing varieties of the Swedish Select type. This is true for the eastern as well as for the central part of the state. In the northern part of the state, at Eureka, the difference in the yields of these two types is not of significance, at Brookings and Highmore the differences are, however, very pronounced. Even at Eureka, while the differences in the yields of Sixty Day and Swedish Select oats are not great, the yields of the latter variety show a considerably higher degree of variability.

YIELDS AND VARIABILITY IN THE YIELDS OF BARLEY

The yields of barley varieties grown at the three stations show the same trend at the respective locations as those of wheat and oats. They require no further discussion here.

Since, according to Harlan, *et al* ('25), the six-rowed barleys of the Manchuria type yield best in the eastern portion of the northern Great Plains area, while the two-rowed barleys of the White Smyrna type are reported to do

better in the western drier portion of this region, it was deemed advisable to include in this investigation performance records of representative two- and six-rowed varieties. As may be seen from Table II, Odessa, a six-rowed type, outyielded the two-rowed barley for the 21 year period, 1909-1929, by 11.8 bushels at Brookings but by only 4.2 bushels at Highmore; while at Eureka the six-rowed barley was outyielded by the two-rowed type by 1.7 bushels per acre. It was, as has been pointed out previously, necessary at Eureka to make use of the yields of Hannchen instead of those of White Smyrna. The habits of growth of these two varieties are quite similar. With the exception of the returns at Brookings, the differences in the yields of the six- and two-rowed barleys are not very significant. It is interesting to note, however, that the coefficients of variability of the yields of these two types are lower in the central portion of the state for the barleys of the White Smyrna (two-rowed) than of the Manchuria (six-rowed) type. This indicates, even though the differences in the two values are not great enough to be statistically significant, that barleys of the White Smyrna type may, on account of their earlier maturity, be more drought resistant, or in reality more drought escaping, than barleys of the Manchuria type such as Odessa. It is common knowledge that White Smyrna will frequently produce at least a partial crop under seasonal conditions too severe for the survival of Odessa. Tabulations showing that White Smyrna usually outyielded Odessa in short crop seasons could be presented. On the other hand, White Smyrna lacks yielding ability under favorable conditions; consequently the lighter average returns at two of the three stations.

VARIABILITY IN THE YIELDS OF FLAX

Yields of flax were available for a long enough period of time to be compared with those shown by the cereals at Highmore only. It will be observed from Table II that the degree of variability shown by flax is considerably higher than that shown by any of the cereals. Flax, as has been brought out by Rotmistroff's ('26) investigations, has a relatively shallow root system; consequently it is dependent on surface moisture or on precipitation during the growing season to a greater extent than the deeper rooted cereal crops. Furthermore, since young flax plants are rather tender and slower to establish themselves than the cereals, they are more susceptible to unfavorable environmental factors.

DEGREES OF CORRELATION IN THE YIELDS OF SEPARATE CROPS

In a previous paper (Klages, '30) it was pointed out that the states of the Great Plains show higher values as a rule for the coefficients of correlation between the yields of individual crops than states to the east of this area. High coefficients for the western states were in evidence especially in the correlations of the yields of those crops growing throughout the same part of the seasons or for such crops having similar vegetation rhythms.

TABLE IV. *Correlations of yields of separate crops and varieties of crops grown on variety test plats at Brookings and Highmore, South Dakota, 1905-1929, as expressed by the coefficient of correlation*

Crops and varieties grown	Crops and varieties grown				
	Common spring wheat ¹	Six rowed barley Odessa	Two rowed barley ²	Early oats, Sixty Day	Late oats, Swedish Select
Brookings					
Durum wheat, Kubanka..	.676 ± .073	.753 ± .058	.649 ± .078	.523 ± .098	.730 ± .063
Common spring wheat ¹ ..		.592 ± .088	.561 ± .092	.225 ± .128	.435 ± .109
Six rowed barley, Odessa..			.856 ± .036	.503 ± .101	.579 ± .090
Two rowed barley ²615 ± .084	.506 ± .100
Early oats, Sixty Day...					.748 ± .059
Highmore					
Durum wheat, Kubanka..	.861 ± .035	.726 ± .064	.698 ± .069	.714 ± .066	.739 ± .061
Common spring wheat, Preston.....		.877 ± .031	.760 ± .057	.737 ± .062	.760 ± .057
Six rowed barley, Odessa..			.912 ± .023	.920 ± .021	.795 ± .050
Two rowed barley, White Smyrna.....				.851 ± .037	.729 ± .063
Early oats, Sixty Day...					.865 ± .031

¹ Brookings, Preston 1905-1912, Marquis 1913-1929; Highmore, Preston 1905-1929.

² Brookings, Chevalier 1905-1912, White Smyrna 1913-1929; Highmore, White Smyrna 1905-1929.

Table IV gives the coefficients of correlation between the yields of the separate crops and varieties, previously considered from the standpoints of yields and variability of such yields at Brookings and Highmore for the 25 year period, 1905-1929. It will be seen that the values for "*r*" are higher for Highmore than for Brookings in all cases but one, and there the difference is small. This bears out the point made in the previous paper. Climatic conditions favoring one crop in the central portion of South Dakota prove favorable to other crops to a greater extent in this area than in the eastern more humid section of the state. Likewise, conditions leading to a reduced yield of one crop are likely to result in reduced yields of other crops to a greater extent in the central portion of the state, with its more rigorous and often erratic climate, than in the eastern portion, with its more humid and more uniform climatic conditions. This is true especially, as may be seen from Table IV, for those crops with critical periods during the same part of the growing season, such as barley and early oats, common spring wheat and oats, or hard red spring wheat and barley. The term critical period is here used as by Azzi ('20) to designate those phases in the development of a crop when it is more susceptible to unfavorable environmental factors than during others.

SUMMARY

I. The yields of wheat, oats, and barley from variety test plats at three stations of the South Dakota Agricultural Experiment Station, Brookings,

Highmore, and Eureka, located in the extreme east-central, central, and north-central portions of the state respectively, were analyzed from the stand-points of average yields, seasonal variability in such yields and degrees of correlation existing between the yields of separate crops.

2. The yields of all crops considered were lower at the two stations in the central part of the state than at Brookings in the eastern portion of the state, while the degrees of variability of such yields were higher in the former than in the latter section. This reflects directly on the greater hazards encountered in crop production in the central than in the more humid eastern portion of South Dakota and no doubt also in other states of the Great Plains area.

3. The range of adaptation of durum wheat is indicated by the fact that the differences in the yields as well as in the fluctuations of such yields, as measured by the coefficient of variability, shown by this crop at the various stations, was less than that shown by any other crop considered in this investigation. The differences in the yields of the hard red spring and durum wheats were greater in the central than in the eastern part of the state. The greatest difference in the variability of the yields of any one crop grown in the two sections of the state were shown in the case of winter wheat; the coefficient at Brookings was 48.45 ± 5.61 as compared to 110.13 ± 19.44 at Highmore.

4. The fact that early maturing varieties of oats are better adapted to South Dakota conditions is indicated not only by their higher average yields but also by a lower variability of yields than that shown by later maturing types.

5. Six-rowed barleys of the Manchuria type greatly outyielded the two-rowed barleys of the White Smyrna type in the eastern part of South Dakota. At the two stations in the central part of the state the differences in the average yields of these two types were small, the two-rowed types showed, however, a somewhat lower degree of variability in their yields than the six-rowed types.

6. The yields of flax in the central part of the state fluctuated more than those of any other crop with the exception of those of winter wheat.

7. Higher degrees of correlation between the yields of separate crops were in evidence in the central than in the eastern part of the state. Conditions leading to either high or reduced yields in one crop in the central part of the state affect the yields of other crops to a greater extent in this than in the eastern portion of the state.

8. The thesis advanced in a previous paper (Klages, '30), based on average yields and variability of such yields of various field crops produced in quantity in the states of the Mississippi Valley, is substantiated in every respect by the findings of this investigation dealing with the same factors but confining itself to specific yields of cereal crops obtained at definitely located stations in the eastern and central parts of South Dakota. The fact that a crop or a group of crops is well adapted to a given area or region is shown

by uniformly high average yields with a minimum of variability in seasonal yields, or in other words, in locations where environmental factors approach the theoretical ecological optimum average yields are high while the degrees of variability of such yields are low.

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SALINITY DEATH-POINTS OF THE OYSTER DRILL SNAIL, *UROSALPINX CINEREA* SAY

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Although many investigators have studied the adaptation of organisms to varying salinities (Beudant, 1816; Plateau, 1883; Bert, 1883; de Varigny, 1883; Yung, 1885; Eisig, 1887; and Frédéricq, 1889), the mechanism for this adaptation (Duval, '25), the relation between the environmental salinity and the salt content of blood (Garrey, '15), the importance of salinity as a barrier to the multiplication and distribution of a species (Colgan, '10; Barrows, '17; and Pearse, '26), and the lethal salinities for several species (*see* Duval, '25, for complete bibliography), no attempt so far as I know has been made to correlate the death-point salinity with the salinity of the environmental waters. While engaged in a study of the natural history of *Urosalpinx cinerea* for the United States Bureau of Fisheries, certain data on the resistance of *Urosalpinx* to low salinities were collected. Three sets of observations are available, one gives the results of a preliminary experiment made at Norfolk, Virginia, during the summer of 1927; the other two sets, collected at Beaufort, North Carolina,¹ are more complete and permit of more accurate analysis.

The literature on the relation between salinity and the distribution of *Urosalpinx cinerea* is very limited. Moore ('11) stated that in Delaware Bay the oyster drill does not thrive at specific gravities below 1.012 to 1.013 (salinity: 15.50–17.00 parts per mille); and in 1923 Nelson gave the minimum salinity for the survival and reproduction of this gastropod in New Jersey as 18.33 parts per mille, a figure that has recently (1928) been lowered to 15.00 parts per mille (private communication). At Hampton Roads, according to my own observations made in 1927, the snail does not normally inhabit waters of salinities below 15.00 parts per mille. What the upper salinity limit may be is shown by observations made at Beaufort, North Carolina, where drills were found living and reproducing in areas where the summer salinities run as high as 37 parts per mille for several days (summer, 1928).

EXPERIMENTS AT NORFOLK, VIRGINIA, 1927

During the summer of 1927, preliminary experiments to determine the lower lethal salinity were made at Norfolk, Virginia, on snails collected from

¹ I wish to take this opportunity of thanking Dr. S. F. Hildebrand, Director of the United States Fisheries Biological Station, Beaufort, North Carolina, for his hospitality and assistance during my stay there.

Hampton Roads. The animals used were taken from 2 localities, the June salinities of which averaged, respectively, approximately 15.00 and 20.00 parts per mille. They were kept in the laboratory for about 6 weeks where the salinity was taken daily and where it never rose over 20 parts per mille. The 2 sets of drills were mixed, and specimens for experimentation were taken at random.

The procedure was as follows: Salinities between 5.00 and 17.00 parts per mille at intervals of approximately 2.00 parts per mille, obtained by diluting sea water with distilled water, were used. The snails (20 at each salinity) were immersed in the water and kept submerged by means of a wire screen stretched below the surface. The jars (of approximately 2 liters capacity) were kept loosely covered to prevent excessive evaporation, and the water was oxygenated twice daily by vigorous stirring. That this was sufficient is shown by the fact that drills will live in jars of sea water for several months without change of water or oxygenation. Temperature, salinity and pH were taken daily, and the condition of the animal noted. The criterion of death was whether or not the mantle would respond to a needle prick. When an animal was found that did not respond to this stimulus it was removed from the experimental jar and placed in running sea water to determine whether it would recover. In every case the animal would, by putrefying within a few days, give conclusive evidence that water of that salinity was lethal to the specimen. Death was always preceded by the animal becoming unattached, and at the lower salinities the animal swelled and protruded from the shell before dying, due undoubtedly to the difference in osmotic pressure. The animals were kept under observations for 10 days, at the end of which time the surviving drills were returned to running sea water and their activity noted. Three different sets of observations with control experiments comprise these experiments (Table I).

TABLE I. *Effects of varying degrees of salinity on Urosalpinx cinerea from Hampton Roads, Virginia, summer, 1927. Salinity in parts per mille*

Experiment number	Salinity at which drills were killed	Percentage of deaths after 10 days	Salinity at which drills survived	Percentage survival after 10 days	Percentage of deaths in control	Average temperature, ° C.	Average pH
1	10.12	90	12.26	95	10	26	8.0 to 8.1
2	12.52	75	15.05	90	5	26	8.0 to 8.2
3	11.35	90	13.91	85	15	24	7.9 to 8.2

EXPERIMENTS AT BEAUFORT, NORTH CAROLINA, 1928

During the summer of 1928 experiments similar to those mentioned above were made on drills collected at Beaufort, North Carolina, where the summer water salinity rose as high as 37 parts per mille and remained well over 30

for the entire season. The following modifications were made in the procedure as given for the Norfolk experiments: (1) the water was oxygenated by bubbling a continuous stream of air through it; (2) instead of using the mantle as a criterion of death, the tip of the siphon was employed for this purpose. The results, which are preliminary, are given in Table II. The pH values, which are rather high, remained with but small variations between 8.4 and 8.8. The continuous stream of air through the sea water brought about a small increase in the pH during the first 24 hours, after which it remained constant. For this reason the animals were not introduced into the jars until the second day.

TABLE II. *Effects of varying salinity on Urosalpinx cinerea from Beaufort, North Carolina, summer, 1928. Salinity in parts per mille*

Experiment number	Salinity at which drills were killed	Percentage of deaths after 10 days	Salinity at which drills survived	Percentage survival after 10 days	Percentage of deaths in control	Av. temp. ° C.	Av. pH
1a	12.81	95	16.89	90	10	26	8.4-8.8
2a	14.45	90	16.22	85	10	26	8.6-8.8
3a	16.00	70	17.43	100	15	24	8.4-8.8

CONCLUSIONS FROM NORFOLK, 1927, AND BEAUFORT, 1928, EXPERIMENTS

Before describing the more detailed Beaufort experiments made during the spring and summer of 1929, certain conclusions derived from the above results should be given. In order to do so a word of explanation is needed concerning columns 2 and 4 in Tables I and II. Column 2 gives the experimental salinity at which at least 50 per cent of the drills died, column 4 gives the next highest salinity in the experiment at which not more than 10-15 per cent of the animals died. I have arbitrarily taken the mean of the figures in columns 2 and 3, and called this the salinity death-point. I believe that the nature of the experiments and results justify such a procedure. This method gives as close an approximation to the salinity death-point as can be gotten even by reducing the intervals between the salinities used.

If the results given in Tables I and II are analyzed according to the method just indicated, the results obtained are these: *Urosalpinx cinerea* collected from Hampton Roads in 2 regions having respectively the following average summer salinities, 15 and 20 parts per mille, have a salinity death-point of approximately 12.50 parts per mille. On the other hand, animals collected from Beaufort where the summer salinity is well over 30 parts per mille have a higher salinity death-point, *i.e.*, 15.60 parts per mille.

The discrepancy between the death-point salinity and the salinity below which drills do not occur in the field at Hampton Roads can easily be ex-

plained after a study of the variations in the salinity of this region occurring throughout the year. During March, April, and early May (1927) the salinity at Craney Island dropped below 12.00 parts per mille for several days, although during the summer and winter months it averaged over 17.00 parts per mille (Federighi, '30). Thus, although the survey during June, 1927, showed that the drills are not found below a salinity of 15 parts per mille, this is not the minimum salinity for survival, since during the spring the salinities of these areas fall as low as 13.00 parts per mille, a figure sufficiently close to the experimentally determined salinity death-point (12.50 parts per mille).

EXPERIMENTS AT BEAUFORT, NORTH CAROLINA, 1929

During the summer of 1929, detailed experiments were conducted at Beaufort to check the observations made in 1927 and 1928. For this purpose a total of 3,290 animals were used at salinities ranging from 8.00 to 35.00 parts per mille. Of this total number, 140 drills were from Hampton Roads (Series 8), the remainder (3,150) were collected at Beaufort. The procedure was essentially the same as that employed for the preliminary Beaufort experiments. In these studies 50 drills were placed in each jar containing 2 gallons of sea water of the desired salinity. The water was kept oxygenated by running a continuous stream of air through it. Each day the drills were examined and the number of dead in each of the jars noted. In all, 8 series of experiments were run. The detailed procedure for each series is given in the following paragraphs.

In series 1, 2, 3, and 4 the salinities ranged from 9 to 34 parts per mille at intervals of less than 2 parts per mille. In all, these involved the use of 1,350 animals. The results may be summarized as follows: below a salinity of 15 parts per mille, over 50 per cent of the drills were killed. The optimum range seemed to be between 17 to 22 parts per mille, where the number of deaths remained less than 15 per cent. Above a salinity of 23 parts per mille the number of deaths again increased to over 50 per cent. These results seemed peculiar in view of the fact that at Beaufort, where these drills were collected, the salinity only rarely fell below 20, and usually remained above 30 parts per mille. This indicated that other factors besides salinity must be involved in the deaths at salinities above 23 parts per mille.

One of the factors that might contribute to the death of the drills at salinities above 23 parts per mille is the rapid reproduction of plankton and its subsequent death and putrefaction, which might so foul the water as to kill the drills. Below 23, the low salinity might act as a retarding factor in the reproduction of the plankton.

In order to test this, 2 types of experiments were run. The first involved the use of sterile glassware, boiled sea water, and drills washed in sterile sea water. Everything was done to keep the initial plankton count to a minimum. If the putrefaction of the plankton were a contributing factor to the death of

the drills at the higher salinities, we should find that, with the above precautions, the number of deaths at salinities above 23 parts per mille would be greatly reduced. Such indeed was the case. In series 5 (Table III) where this was done, deaths to the number of 50 per cent occurred only at salinities below approximately 16.7 parts per mille. At the higher salinities the percentage of deaths only rarely exceeded 15 per cent.

TABLE III. *Effects of varying salinity on Urosalpinx cinerea from Beaufort, North Carolina, and Hampton Roads, Virginia, summer, 1929. Salinity in parts per mille*

Experiment number	Salinity at which drills were killed	Percentage of deaths after 8 days	Salinity at which drills survived	Percentage survival after 8 days	Percentage of deaths in control	Av. temp. ° C.	Av. pH
5	15.25	94	18.25	94	2	23	8.6
6	16.64	92	18.87	82	12	23	8.5
7	16.51	76	19.93	86	12	22	8.6
8	10.63	100	12.79	75	0	25	7.9

Another way to test the above assumption is to change the sea water (of the proper salinity) in each jar daily. In series 6 and 7 (1,200 animals) this was done, and again only salinities below approximately 18 parts per mille were fatal (Table III).

The observations made during 1929 on the drills from Hampton Roads showed that the lower limit for survival of the snail is approximately 11.70 parts per mille, a result similar to that one obtained during the summer of 1927 (Table III).

DISCUSSION

The preceding data show that the salinity death-point of *Urosalpinx cinerea* is influenced to a great extent by the environmental salinity. Drills collected at Norfolk from localities having salinities of approximately 15 and 20 parts per mille show lethal salinities of approximately 12.50 parts per mille (Table I) and 11.70 (Experiment 8, Table III). On the other hand, snails collected at Beaufort with an environmental salinity of approximately that of sea water (over 30 parts per mille) for most of the year, show a lethal salinity of 15.60 (Table II) and 17.60 parts per mille (Experiments 5, 6 and 7, Table III).

In this connection it is interesting to draw attention to one fact which these results bring out. The extent of adaptability, or the salinity factor of safety, becomes smaller as the animal becomes adjusted to lower salinities. Thus at Hampton Roads a drop of from 8 to 9 parts per mille (at the maximum, from 20 to 12) was fatal, while at Beaufort a decrease of over 15 parts per mille in the salinity of the waters was necessary for death (from 30 to

approximately 16). This lower factor of safety in an animal that has become adapted to lower salinities may become of biological importance in its distribution. For instance, heavy rains in the areas drained by the Elizabeth, Nansemond and James Rivers might reduce the salinity of the Hampton Roads region sufficiently to kill great numbers of *Urosalpinx cinerea* infesting oysterbeds in this locality.

The relationship between environmental salinity and salinity death-point is similar to that reported by other investigators between environmental temperatures and lethal temperatures. Davenport and Castle (1895) reported that toads reared at various temperatures had different heat rigor temperatures. Those reared at higher temperatures (24° – 25° C.) could resist a temperature higher by 3.2° C. In 1899 Vernon reported that the death temperature of marine animals in the Mediterranean Sea varied through the season, being higher during the summer months. He wrote "in eight of the nine observations made, the death temperature had increased, so there can be no doubt that a certain degree of acclimatization to high temperature had been effected by the warmer temperature of the animals environment." These results were corroborated by Mayer ('14) who stated that *Aurellia aurita* at Halifax ceased "to pulsate at 29.4° C. at which temperature it is most active at Tortugas, Florida; and conversely, the Tortugas medusæ cease to pulsate at about 7.75° C., while those from Nova Scotia continue to move at a temperature of -1.4° C." Similar observations have been made by Hathaway ('28) on fishes and amphibians.

As regards the decrease in the factor of safety with the acclimatization to lower salinities, it is interesting to quote Mayer ('14), "It appears probable that *Aurellia* is a boreal or arctic animal which has wandered into the tropics and become fairly well acclimated, although living in these warm waters within 9° C. of its death-temperature. Thus, in comparison with their northern relatives, these *Aurellias* in the tropics are poorly adjusted to their temperature environment, and a change of even 2° or 3° above their normal temperature causes a decided lassitude and loss of rate in pulsation. We see, therefore, that the medusa has become adapted to a tropical environment, but this has been accomplished at the expense of its factor of safe adjustment to temperature changes." It may be argued similarly that *Urosalpinx cinerea* was originally a marine form which has invaded the brackish waters and so reduced its factor of safe adjustment to salinity changes.

There remains the problem of how this adaptation to lower salinities has taken place. Two explanations are possible. One states that the adaptation takes place through the survival of those forms better fitted to the new environment, and the other, supported by the experimental evidence of Davenport and Castle (1895), maintains that adaptation may take place "without selection, purely by the capacity of individual adaptation which organisms possess." This is a problem for future experimentation.

SUMMARY

Oyster drills (*Urosalpinx cinerea* Say) collected from areas in Hampton Roads, Virginia, where the summer salinity was 15 and 20 parts per mille, had salinity death-points of 12.50 and 11.70 parts per mille. On the other hand, snails collected at Beaufort, North Carolina, where the environmental salinity is over 30 parts per mille, showed lethal salinities of 15.60 and 17.60 parts per mille. This is interpreted to mean that the environmental salinity influences the death point salinity, although the relation is not directly proportional, since, as the animal becomes adapted to lower salinities, the salinity factor of safety (the difference between the average environmental salinity and the death point salinity) becomes smaller.

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EFFECT OF ENVIRONMENTAL FACTORS ON THE WOOD STRUCTURE OF LODGEPOLE PINE, *PINUS* *CONTORTA* LOUDON

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INTRODUCTION

That environmental factors affect the structure of the leaves of plants is well known, and a considerable literature has grown up around the development of that fact. Some investigations have proven that such factors also measurably affect the cellular structure of the wood of trees (Adams, '28, Cieslar, 1897, Geiger, '15, Hartig, '01). Other investigations cast doubt upon this assumption (Harlow, '27). Moreover, the exact correlation, if any, of variations in cell structure with measured factors of the habitat has been investigated in but few instances. That such a probable correlation is of scientific and economic value is shown by the increased attention being given to this subject by the United States Forest Products Laboratory (Koehler and Paul, '29, Paul, '30) and the Canadian Forest Products Laboratory, as well as by research workers in the educational and research institutions of this and other countries.

While studying the vegetation, successional relations and environmental factors of an isolated lava bed in the Cascade Mountains of southwestern Washington, in contrast with the vegetation just off the lava bed, an excellent opportunity presented itself for studying not only the growth rates of the trees, but also the effect of the severe conditions of the lava bed on the minute structure of the wood of the trees. For this purpose specimens of the wood of several species of trees growing on the lava bed and just off the lava bed were obtained and a study made of their structure. The general vegetational and environmental conditions obtaining on and off the lava bed will be discussed elsewhere,¹ and the purpose of this article is to record the results of a study of the wood structure of one of the tree species, the lodgepole pine (*Pinus contorta* Loudon), as affected by varying site factors. The wood of lodgepole pine growing in sphagnum bogs in the same region was also included for the sake of comparison.

REVIEW OF LITERATURE

The earliest investigations of wood structure were concerned with the average size and the degree of variability of the different elements of the

¹ To appear later under the title "Vegetation of a Lava Flow in the Cascade Mountains of Washington."

wood, chiefly for the purpose of wood identification. With increasing information came the realization that the wood elements vary from tree to tree and that they vary even more widely in different parts of the same tree.

But, until relatively recent times, there has been very little attempt to determine the effect of different environmental conditions on the cellular structure of wood. Naturally the first criteria investigated were the technical properties of the wood, such as specific gravity, hardness, resistance to bending, etc. Only when it was understood that these technical properties are dependent upon the structure of the cells was an attempt made to determine the effect of specific environmental factors on the size, composition and relative proportion of the different types of cells found in wood. Essner (1886), investigating the medullary rays of spruce trees, found that trees growing under favorable conditions had a smaller number of rays per unit area than those growing under unfavorable conditions. The work of Hartig, summarized in his later publication ('01), is the earliest extensive series of investigations of quality and structure of wood in relation to environment. He found that the most favorable growth conditions, *i.e.*, full light, large crown, rich soil and not too high a rate of transpiration, produced wood of maximum strength and weight.

Mell ('10) was one of the first in this country to point out that the "quality of locality" could be determined by the average length of the fibers of California walnut wood (*Juglans californica*). The longest fibers (1.554 mm.) being found in trees growing on rich, moist soil, whereas those growing on dry, gravel soil had shorter fibers (1.302 mm.).

Considerable work has been done to determine the effect of site on the quantity and quality of lumber produced. This has been discussed by various authors (Koehler and Paul, '29, Paul, '30) and will not be treated here. The specific weight of wood is very distinctly affected by environmental factors. In general, there is no direct relation between specific gravity and width of ring; but, when growth is retarded or accelerated due to crowding followed by thinning, the narrower rings have a lower specific gravity (Paul, '30). Thus silvicultural treatment overshadows the effect of soil, moisture, and other physical factors of the environment. Poor growing conditions during the summer, generally due to lack of moisture, tend to produce relatively less summer wood, hence cause a decrease in specific gravity (Paul, '30). In southern yellow pine (*Pinus palustris*) there is a close and direct relation between the amount of summer wood and the amount of available moisture. On dry sandy soil shortleaf pine (*Pinus echinata*) produced wood with a specific gravity 15 per cent lower than that on clay loam soils. Annual burning, acting on the fertility and water holding capacity of the soil, likewise lowered the specific gravity. Crown size and density of stand are of importance (Paul, '30). "The specific gravity of white cedar (*Thuja occidentalis*) grown on limestone soil is somewhat greater than that of the same species from a peat bog" (Harlow, '27).

The mechanical properties of wood have been the subject of investigation, particularly by Janka ('13), who found no relation between ring width and specific gravity or resistance to crushing, etc. This resistance is due rather to relative proportions of spring wood and summer wood in the rings. Redwood (*Sequoia sempervirens*) from small-crowned trees in dense stands has a higher resistance to compression parallel to the grain than redwood from large-crowned trees in open stands (Paul and Luxford, '18).

The chemical composition of wood varies with growth conditions. Cieslar (1897) found that spruce (*Picea excelsa*) grown under optimum conditions in its own range contained more lignin than in milder localities outside its range, or at higher elevations.

The length of the various elements in the wood have been more thoroughly investigated than any other single criterion. "The tracheids of trees growing in rich, moist soil are usually longer than those of trees growing in dry soil" (Mell, '11). Lee and Smith ('16) found the tracheids of Douglas fir (*Pseudotsuga taxifolia*) from trees growing in the coast region of British Columbia to be slightly longer than those growing in the mountains. The coast trees were growing at 100 feet elevation with 60 inches of rainfall and in good sandy clay loam soil, whereas the mountain trees were growing at 4,000 feet elevation, with 18 inches of rainfall and in coarse shallow gravelly clay overlying rocks. Harlow ('27) compared the wood of white cedar (*Thuja occidentalis*) from peat bogs with that from limestone soil, and found a slight though not significant difference in tracheid length, tracheid width and ray volume. Adams ('28) found an increase in the average size of the tracheids of jack pine (*Pinus banksiana*) with increase in spacing and consequent decrease in competition. Shope ('27) found an increase in the average size of the tracheids (10 per cent increase in volume) and tracheae (15 per cent) of aspen (*Populus tremuloides*) in Colorado with increased elevation of habitat (5,800 feet to 9,000 feet). MacMillan ('25), investigating tracheid length in red spruce (*Picea rubra*), reports a greater average tracheid length in free growing trees (2.79 mm.) than in suppressed trees (2.52 mm.). He, however, found no difference in the length of tracheids from the northern and southern limits of the range of red spruce.

The relation between fiber length and the strength of wood seems indeterminate (Gerry, '15), though there is a distinct relation between thickness of wall of summer tracheids and strength (Gerry, '16). The usefulness of wood for paper pulp increases with increase in length of fiber, other things being equal (Gerry, '15). The longest tracheids are said by Gerry ('15, '16) to be in the earliest cells of the spring wood and the shortest in the summer wood. In loblolly pine the lengths are: spring wood tracheids, 3.03 mm., summer wood tracheids, 2.69 mm. Lee and Smith ('16) find no great difference in length between spring and summer wood tracheids; if anything, the summer wood tracheids are slightly longer. This is the case also with jack pine (Kribs, '16).

There seems to be no relation between width of ring and the dimensions of the tracheids in Douglas fir and longleaf pine (*Pinus palustris*) (Gerry, '16), though Adams ('28) reports that "the width of the annual ring for any year is dependent on the size as well as on the number of tracheids produced during the year." The greater the height growth the greater the fiber length, according to Lee and Smith ('16) and MacMillan ('25). Adams ('28), however, found that the "length of an internode is not dependent on the length of the tracheids produced." This difference may be due to differences in the age of the trees investigated. In old Douglas fir (455 years) there was no evidence in the length of the tracheids of a decline due to old age (Gerry, '16). MacMillan ('26) also reports a gradual increase, with fluctuations, in tracheid length with increasing age of the tree up to the age of 210 years, the oldest trees used.

The number and size of the medullary rays in wood has been summarized by Weinstein ('26) and Meyer ('22). Geiger ('15), working with teak (*Tectona grandis*), found a difference in number and size of medullary rays in East Java and West Java which he attributes to climatic differences. He says trees on good calcareous loam had rays 95 cells high, whereas those on poor calcareous loam had rays only 37 cells high. Meyer ('22) maintains that specimens of ash (*Fraxinus*, species not given), tulip poplar (*Liriodendron tulipifera*) and bald cypress (*Taxodium distichum*) growing in lowlands have greater ray volume than the same species growing on higher ground. The severe conditions obtaining at high altitudes in the mountains of New Hampshire reduce the medullary ray tissue very greatly as compared to closely related species at lower elevations (Forsaith, '20). Shope ('27) found no such reduction in the amount of medullary ray tissue in aspen in Colorado at 9,000 feet elevation as contrasted with 4,800 feet elevation.

ENVIRONMENTAL FACTORS

Only a brief summary of the environmental factors obtaining in the region under discussion will be given here.

The Goose Lake lava bed is 10 by 5 miles in extent, and is located on the Columbia National Forest in the Cascade Mountains of southwestern Washington at an average elevation of 3,000 feet (Fig. 1).

No rainfall records are available for this immediate locality, but there are records for the Wind River Forest Experiment Station about 15 miles to the southwest, and at an elevation of about 1,000 feet. A 15 year summary, 1911-1925, gives an average yearly rainfall of 86.03 inches, 51 per cent of which falls during November, December and January, and only 13 per cent during May to September inclusive. The amount of rainfall decreases very rapidly as one goes from west to east over the Cascades. The lava bed, located as it is over toward the dry side of the Cascades, probably has a somewhat lesser rainfall than the Wind River Station. In any case, the rainfall would be uniform for both the lava bed and the virgin timber immediately off the bed.

The mean annual temperature at the Wind River Station (1911-1925) is 48.0° F., with the months of May to September inclusive having a mean above 50° F. Temperatures taken during the summer of 1928, from July 10 to August 19, gave an average maximum air temperature of 82.7° F., and a minimum air temperature of 44.3° F. on the lava bed, in contrast with which the air temperature in the virgin timber just off the lava bed was:

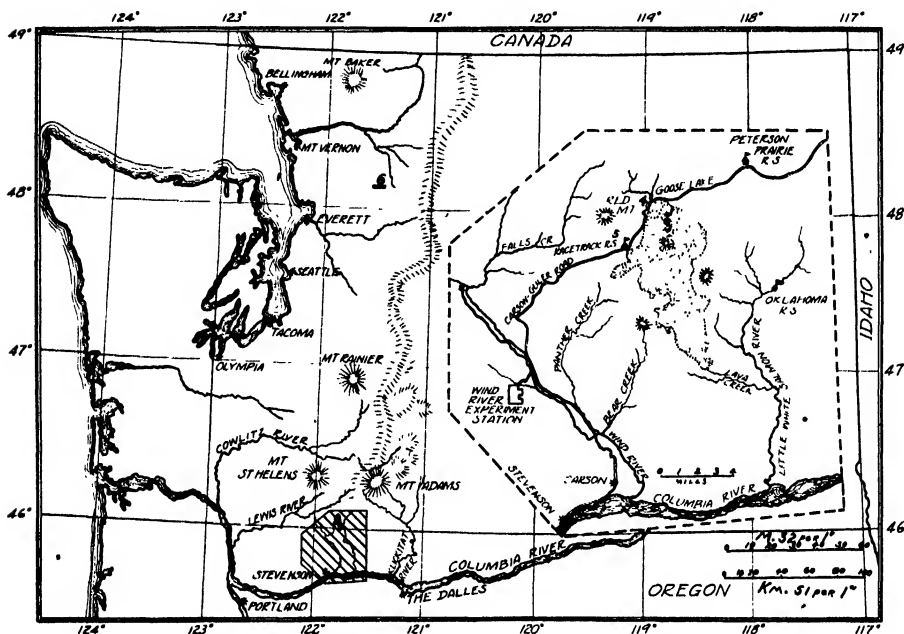


FIG. 1. Map of the State of Washington showing areas where wood specimens were secured. Inset is map of lava bed and vicinity. Numbers indicate: (1) lava blocks forest, (2) lodgepole pine forest, (3) mixed forest, (4) dense virgin timber forest, (5) open second growth forest, (6) sphagnum bog.

maximum 70.3° F., minimum 47.8° F. The average maximum soil surface temperature on the lava bed was 111.7° F. This shows the lava bed to be hotter during the day and colder during the night than the adjacent virgin timber.

Evaporation, as measured with Livingston white spherical atmometers, shows a daily average of 26.18 c.c. on the lava bed and 15.92 c.c. in the adjacent virgin timber.

The insolation is very much more severe in the open stand of lodgepole pine trees on the lava bed than in the dense virgin timber. The average daily excess of the black bulb over the white was 12.95 c.c. on the lava bed and practically zero in the virgin timber. The above mentioned factors, coupled with a rather light, often extremely shallow soil overlying the rock of the lava bed cause a gradual drying out of the soil, particularly the surface layers.

Soil at greater depths was not examined. Soil under the virgin timber was deep and well supplied with water late into the season, and the virgin timber trees probably did not suffer from the lack of it.

The sphagnum bog habitat was not studied by the author, and the following is taken from Rigg's ('16) review of the work of Cox on the temperature conditions in the cranberry bogs of Wisconsin. The conditions as compared to those on adjacent hard land probably present in general an accurate picture of the conditions in the sphagnum bogs of Washington. In the main, conditions for plant growth are less favorable in the bog than on hard land. This applies to both soil and air temperature and the difference between soil and air temperature. Relative humidity is higher and wind movement less in the bog than on hard land adjacent, hence evaporation rates are not as great.

No data are available on the acidity or toxicity of the water in the Kirk Lake Bog at the point where the trees examined were growing. The comparatively rapid rate of growth of the trees in the sphagnum bog would seem to indicate that the acidity or toxicity of the water was slight and that the supply of water was plentiful.

MATERIAL USED

On the lava bed there are three distinct forest types representing distinct stages in the process of revegetation of the lava bed and the volcanic ash which covers part of it. These are: (1) the lava blocks forest, (2) the lodgepole pine forest, and (3) the mixed forest (Fig. 1).

The first of these is an area composed of a jumble of lava rocks of all sizes with very little soil except in the crevices of the rocks. The trees are very wide apart and are chiefly alpine fir (*Abies lasiocarpa*) with a few scattered trees of other species. Two lodgepole pines were collected on this area. Tree number three was 36 years old, 96 mm. in diameter at a stump height of 2 feet, and was 18 feet high. Number 4 was 106 years old, 130 mm. in diameter at 2 feet, and 51 feet high.

The greater part of the lava bed is covered by a forest of lodgepole pine. This is an open stand of rather small trees growing in comparatively shallow soil, but apparently under more favorable conditions than the lava blocks forest. In various parts of this forest five trees were felled and wood specimens collected. The field data are as follows:

Tree number	Average diameter at 2 foot level	Age at two foot level	Height of tree
8	274 mm.	121 years	73 feet
12	108 "	122 "	54 "
25	120 "	126 "	46 "
27	248 "	126 "	55 "
32	194 "	123 "	47 "
Average	189 mm.	124 years	55 feet

This forest gradually gives way to a denser, more mesic forest, dominated by mountain hemlock (*Tsuga mertensiana*) but mixed with many other species, hence called the mixed forest. This is on much deeper soil than the lodgepole pine forest, but in many cases competition cuts down the growth rate. Wood samples from one tree, number 49, were collected from the mixed forest. It was 264 mm. in diameter, 189 years old at the two foot level and 68 feet high.

The three forest types discussed above are all growing on the lava bed and subject to its more severe environmental conditions so that they can be and are here discussed together under the name of the lava bed forest. However, the greater openness, shallower soil and probably higher evaporation rates make conditions most severe on the lava blocks area, while the increasingly deeper soil, denser stand and more mesic conditions generally make for an increasing and more dependable water supply in the lodgepole pine, and mixed forests. Growth conditions are therefore better in these forests. This is borne out by the fact that in the case of nearly all of the criteria of comparison used in this study, namely, in total width of ring, per cent of summer wood, radial diameter of spring and summer wood cells, and tangential diameter of summer wood cells, the trees on the lava blocks area are lowest, with sometimes lodgepole pine forest next higher and sometimes mixed forest next higher. Mixed forest is often lower than lodgepole pine instead of higher, largely because lodgepole pine is a relict tree in this forest type and the greater density of stand produces a competition which may slow down the growth rate and also affect other criteria.

Two types of forest just off the lava bed were sampled. The type which I have called the dense virgin timber is just off of the lava bed to the north and is a dense stand of western white pine (*Pinus monticola*), Douglas fir, white firs (*Abies* spp.), with some western red cedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*) and mountain hemlock intermixed. In the more open places there is a sprinkling of lodgepole pine, probably relict individuals left over from the revegetation of spot fired areas. The trees were collected on a moderate south facing slope in a fairly dense stand. The field data for each tree follow :

Tree number	Average diameter at 2 foot level	Age at two foot level	Height
101	288 mm.	98 years	102 feet
104	258 "	83 "	87 "
105	246 "	81 "	91 "
106	378 "	105 "	112 "
Average	293 mm.	92 years	98 feet

At the base of Red Mountain just north of the Race Track Ranger station about 4 miles from the lava bed is a considerable area (Fig. 1) in which a field was being cleared as an emergency landing field for fire patrol airplanes.

This cutting made it possible to get a maximum number of stump counts in a minimum amount of time. Because of its character, I have called it the open second growth forest. It is in reality a rather young (about 80 years) second growth stand, but due to insufficient seeding in after an early fire, it is a very open park-like forest. The soil is probably somewhat poorer than that of the dense virgin timber forest discussed above, but the open character of the stand permits a very heavy crown development with branches nearly to the ground. This, together with little or no competition for water, due to wide spacing of the trees, allows for rapid growth and tends to offset the better soil of the virgin timber. These 2 forest types are combined under the heading of virgin timber. The field data for each tree follow:

Tree number	Average diameter at 2 foot level	Age at two foot level	Height
81	238 mm.	63 years	63 feet
82	216 mm.	60 years	57 feet
83	148 mm.	55 years	
Average	201 mm.	59 years	60 feet

The type locality in which Douglas ('14) first collected the lodgepole pine was "In North-West America in swampy ground near the seacoast"—where it is found back of the sand dunes in dense tangles usually not over 30 feet in height. It is also found in western Washington at the edges of the gravelly prairies characteristic of Pierce County, near Tacoma, and in such dry places as the lava bed under discussion. East of the Cascades it forms dense forests on rather dry, sterile soil. Some botanists consider the coastal form and the Rocky Mountain form 2 separate species, while other botanists consider them as one species. Piper ('06), in discussing the vegetation of the sphagnum bogs of western Washington says: "On the drier hummocks . . . one is often surprised to find the black pine (*Pinus contorta*) typically a plant of barren, gravelly or sandy soil." It seemed desirable to determine whether this unusual habitat had any effect on the growth and structure of the wood.

Three trees from the sphagnum bog were sampled. They were obtained for me through the kindness of Professor George B. Rigg, of the University of Washington, from Kirk Lake Bog, 90 miles north of Seattle near Darrington, Washington (Fig. 1). They were growing in a mat of sphagnum which was sampled to a depth of 2 feet and found to be pure sphagnum. The sphagnum mat was probably more than 2 feet deep. The lodgepole pine was co-dominant with white pine, hemlock and red cedar, and was not at all suppressed. The trees were from 40–55 feet in height and formed a rather open stand, with their crowns not touching and spaced from 15 to 20 feet apart. The field data for each tree follow:

Tree number	Average diameter at 2 foot level	Age at two foot level	Height
127	117 mm.	53 years	55 feet
128	94 "	54 "	_____
129	101 "	50 "	_____
Average	104 mm.	52 years	55 feet

All of the data presented in this study were obtained from the 18 trees described above. From each tree a cross-sectional disk was taken at the 2 foot level, and a rough block of wood, the thickness of the disk (2 inches) 2 inches wide and long enough to include the pith and the bark, was cut out along the average radius, which was the average of 4 radii on the disk. The block was properly labeled, and, when ready for study, was trimmed to $\frac{1}{2}$ inch wide, and divided into an upper and a lower half (Fig. 2). The upper

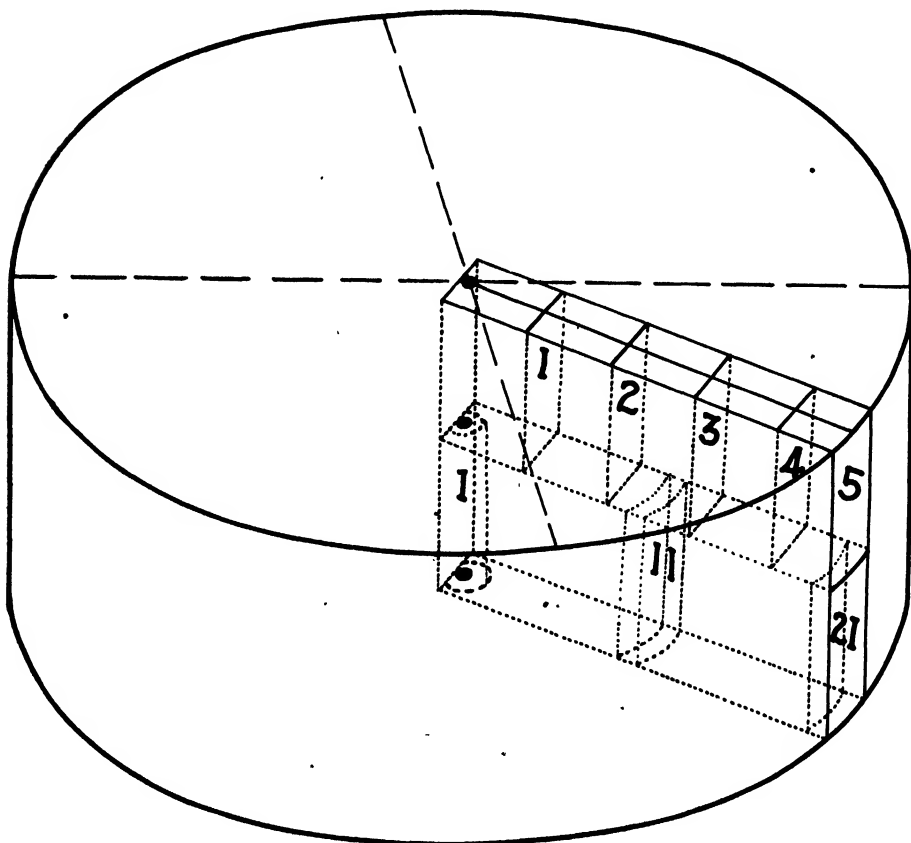


FIG. 2. Diagram of cross-section of tree showing 4 radii measured, average radius laid out, and the block of wood along this average radius which was used in this study. The upper part of the block was used for cross-sectional measurements and the lower part for tracheid length measurements.

half was used for cross-sectional measurements and the lower half for tracheid length measurements.

METHOD OF PRESENTATION OF RESULTS

All of the cross-sectional data are presented as the average for groups of 10 rings each from the pith to the bark. That is, starting at the pith, each individual ring was measured, the first 10 rings were averaged and the result presented as the average for rings 1-10. The same was done successively for each group of 10 rings out to the bark.

Attention should be called to the fact that the data presented in Table I are the averages of the original figures, whereas the graphs, figures 3-7, are based on these same data, but smoothed by the 3-point moving average in order to lessen minor fluctuations in the curves. The curves for tracheid length were not smoothed.

WIDTH OF RINGS—GROWTH IN GIRTH

The upper half of the block of wood along the average radius (Fig. 2) was split into small blocks of convenient size for cutting, numbered consecutively from the pith to the bark, boiled in water to expel the air, and placed in a mixture of alcohol and glycerine until ready for study. No further softening was needed, and sections were cut 30 microns thick, stained in safranin and mounted in glycerine for examination. The total width of the ring was measured with a calibrated ocular micrometer and expressed in millimeters. These sections served also for determining the per cent of summer wood, radial and tangential dimensions of the tracheids, degree of differentiation of spring and summer wood and thickness of the tracheid walls.

The total width of the rings varies greatly from year to year, but when averaged by 10-year periods a distinct decrease with increasing age of the tree is discernible. Sometimes growth is slow for the first few years of the life of the tree, increases for a few years more, but usually by the tenth year the growth rate begins to fall off (Table I). This decrease in growth rate with increasing age is not very rapid for the lava bed trees, probably because of lack of crowding, but for the virgin timber trees a very rapid falling off is noticeable as increased competition with the other trees of the dense virgin stand tend to suppress the lodgepole pine, which in this region may be considered as a relict tree in the climax forest. The same falling off is discernible (Fig. 3) in the sphagnum bog trees. The average annual increment in diameter for the first 60 years (the only period directly comparable because all of the trees examined from the sphagnum bog were young) is: lava bed—1.87 mm., virgin timber—3.80 mm., sphagnum bog—4.02 mm.

This is unusually rapid growth for trees growing in a sphagnum bog, as Rigg ('18) gives the annual increase in diameter of the 9 lodgepole pine trees growing in sphagnum bogs which he measured as 0.78 mm. Professor Rigg

TABLE I. *Summary of the averages of all measurements of lodgepole pine growing in the various major habitats*

Ring number, pith to bark	Total width of ring (millimeters)			Per cent of summer wood			Radial dimension in microns (spring tracheids)		
	Lava bed	Virgin timber	Sphagnum bog	Lava bed	Virgin timber	Sphagnum bog	Lava bed	Virgin timber	Sphagnum bog
1-10	1.438	2.431	2.833	27.8	31.1	34.4	21.7	24.3	23.1
11-20	1.146	2.384	3.018	26.2	28.0	40.3	27.2	26.9	36.0
21-30	.900	1.979	2.209	21.2	23.7	51.5	28.1	33.3	34.7
31-40	.706	1.700	.909	23.9	26.1	44.3	28.1	34.1	33.7
41-50	.736	1.382	1.452	25.4	30.6	52.1	30.3	34.6	33.3
51-60	.699	1.218	1.641	27.4	31.7	45.6	28.9	35.7	40.3
61-70	.546	1.196		26.7	35.0		28.4		
71-80	.453	.376		32.9	34.2		27.8	34.2	
81-90	.406	.202		30.4	37.1		23.9		
91-100	.471	.138		30.1	30.5		27.2	32.1	
101-110	.466	.950		31.9	28.4		30.6		
111-120	.675			29.5			31.9		
121-130	.637			31.6			35.3		
131-140	.507			23.7					
141-150	.500			27.8			32.9		
151-160	.427			32.1					
161-170	.371			32.6			28.1		
171-180	.300			31.3					
181-190	.271			25.8			24.7		

	Radial dimension in microns (summer tracheids)			Tangential dimension in microns (summer tracheids)		
	Lava bed	Virgin timber	Sphagnum bog	Lava bed	Virgin timber	Sphagnum bog
1-10	16.5	16.0	20.7	18.7	20.9	22.5
11-20	16.0	17.8	26.1	21.7	22.3	27.9
21-30	17.6	20.2	25.4	25.5	23.8	29.8
31-40	17.6	20.2	21.2	25.5	26.3	27.0
41-50	17.0	21.2	22.1	25.9	29.5	26.8
51-60	17.0	20.7	24.5	26.6	28.4	30.1
61-70	16.4			26.6		
71-80	15.6	18.6		26.6	28.8	
81-90	15.5			26.2		
91-100	15.6	16.5		26.4	28.0	
101-110	16.2			26.0		
111-120	17.0			26.3		
121-130	20.2			27.9		
131-140						
141-150	16.7			28.6		
151-160						
161-170	15.4			28.6		
171-180						
181-190	14.5			26.5		

has since sent me specimens of lodgepole pine from the Evans Creek Bog some of which show a rapid growth rate, while others show very slow growth. Just what factors cause this difference in growth rate is not known, but the nearness of the trees to a supply of "fresh" water flowing into the

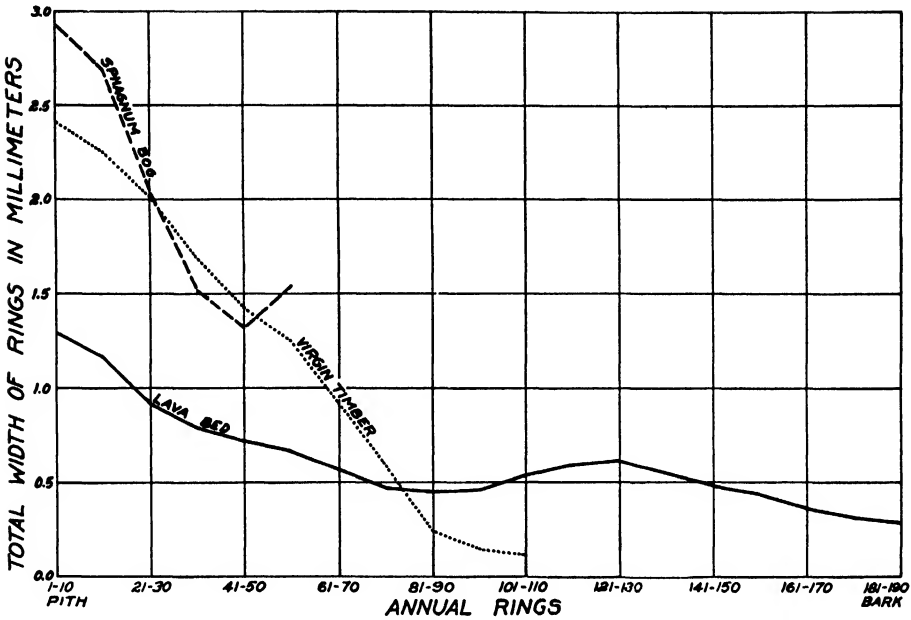


FIG. 3. Total width of the annual rings expressed in millimeters. Average of measurements of all trees from the sphagnum bog, virgin timber, and lava bed habitats, respectively. Curves smoothed by the 3-point moving average method.

bog from a stream or pond seems to be of importance. It would be interesting to determine the effect of this difference on wood structure, but until now no material has been available.

The growth rates of 100 lodgepole pines on the lava bed and in the virgin



FIG. 4. Cross-sectional block of wood cut from a lodgepole pine tree growing in a sphagnum bog. (Tree No. 129, 50 years old, actual length of the radius along pencil mark is 101 mm.)

timber were determined from stump counts and increment borings made in another study. The average annual increment in diameter and the number of trees measured is given below.

Lava bed	38 trees	2.16 mm.
Virgin timber	62 trees	3.84 mm.

From this it will be seen that the growth rate of the trees used in this investigation was normal. It is difficult to arrange the 6 minor habitats in their proper sequence with regard to the rate of growth because of the very rapid early growth rate and very slow later growth rate of the dense virgin timber trees and the sphagnum bog trees as contrasted with the comparatively even growth rate of the open second growth forest trees (Fig. 3).

PER CENT OF SUMMER WOOD

The portion of each ring occupied by summer wood was measured, averaged by groups of 10 rings each, and expressed in per cent of the total width of the ring (Table I). A very distinct difference exists between the trees from the 3 major habitats. The averages for the first 60 years show the lava bed trees to have 22 per cent of each ring given over to summer wood, the virgin timber trees 28.5 per cent, and the sphagnum bog trees 44.7 per cent (Fig. 5).

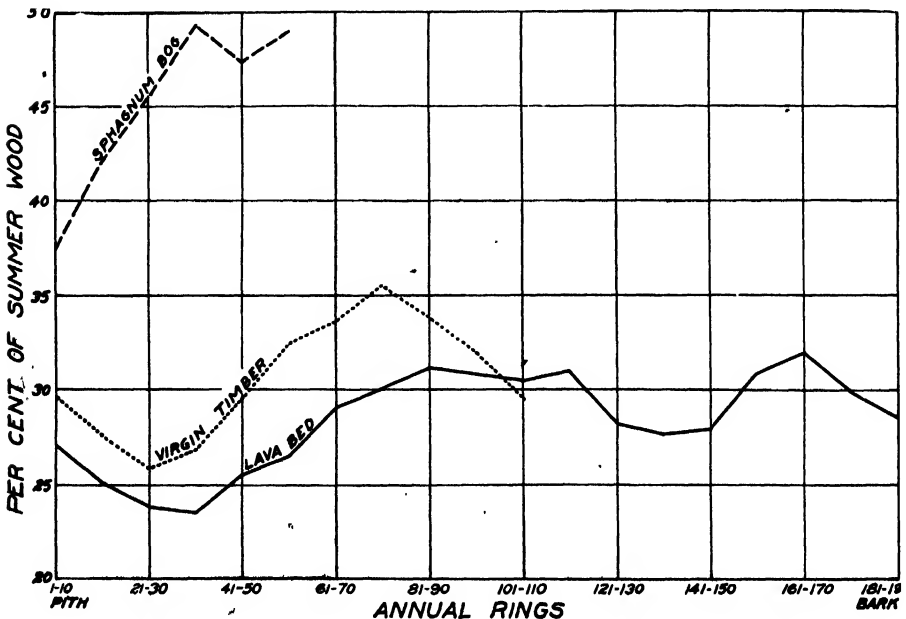


FIG. 5. Amount of summer wood per annual ring expressed in per cent. Average of measurements of all trees from the sphagnum bog, virgin timber, and lava bed habitats, respectively. Curves smoothed by the 3-point moving average method.

When we consider the minor habitat differences we find that the 6 habitats can be arranged in the order of increasing per cent of summer wood per ring as follows: lava blocks forest, lodgepole pine forest, mixed forest, dense virgin timber forest, open second growth forest and sphagnum bog forest.

When conditions in general are favorable for growth, the rings are wide, and after the spring wood has been formed the latter part of the season is spent in laying down a large number of rows of summer wood tracheids, resulting in a large per cent of the ring being dense wood. If, on the other hand, conditions are in general unfavorable for growth, narrow rings are formed, and after the spring wood is laid down there is either little time or little food left with which to lay down a large amount of summer wood, hence a small per cent of dense wood is formed. Whether the growing season is shortened by scarcity of water or other adverse condition, or whether the growing season is as long as in the case of trees with wider rings but the tracheids are formed more slowly, is not known. It seems more likely that the former is true (Paul, '30), and that adequate moisture early in the growing season causes a relatively large amount of spring wood to be formed, but as the season advances drier conditions prevail, particularly in the shallow soiled lava bed habitats, and the formation of summer wood is curtailed. This is in accord with Paul's ('30) work on southern pine.

Although, as we shall see later, the tracheids of the sphagnum bog trees are larger than those of the lava bed trees, the difference in size is not sufficient to account for the difference in width of the rings (compare Adams ('28) and Gerry ('16)). The difference in width is due chiefly to the increase in the number of rows of cells laid down (Table II). This is particularly well shown in the case of the summer tracheids.

TABLE II. *Average number of tracheids in width of spring and summer wood (first 60 rings from pith outward)*

	Width per ring in mm.	Per cent of summer wood	Width of spring wood in mm.	Width of summer wood in mm.	Number of tracheids in width		
					Spring	Summer	Total
Sphagnum bog....	2.01	44.7	1.112	.898	30.0	38.5	68.5
Virgin timber.....	1.60	28.5	1.144	.456	36.5	23.5	50.0
Lava bed.....	0.94	22.0	.733	.207	26.8	12.2	39.0

RADIAL DIAMETER OF SPRING AND SUMMER WOOD TRACHEIDS

In every fifth ring from pith to bark the number of spring and summer wood tracheids in the radial direction covering a convenient number of spaces in the ocular micrometer (usually about 500 microns if the ring was wide enough) were counted and their average radial diameter calculated. The average for every 10 rings was determined in order to make the figures directly comparable with those of ring width and per cent of summer wood.

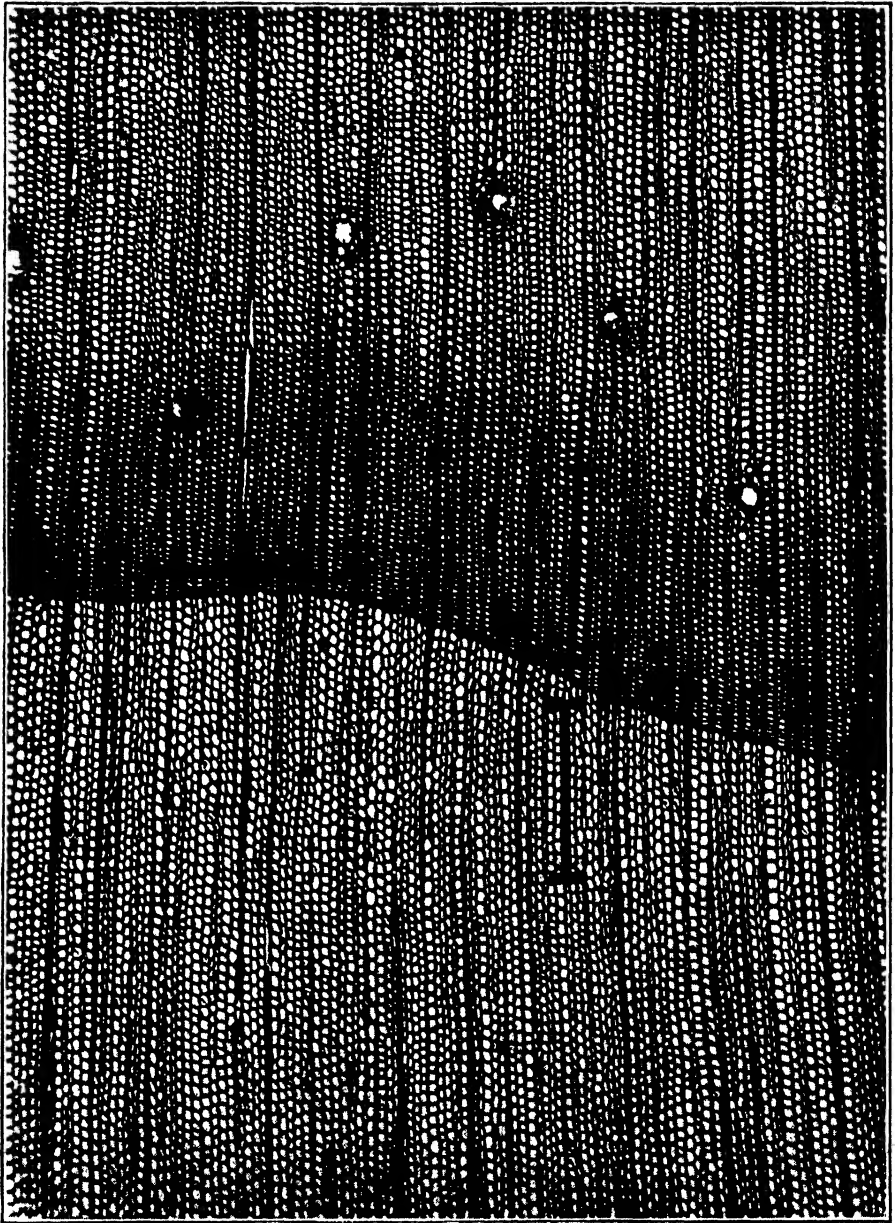


FIG. 6. Cross-section of lodgepole pine wood magnified $\times 50$ showing method of measuring radial and tangential diameter of tracheids. The heavy lines indicate the position and the approximate number of cells (in 500 microns) measured to obtain the radial and tangential diameters of the spring and summer wood tracheids. Photo by courtesy of U. S. Forest Products Laboratory.

SPRING WOOD TRACHEIDS

In the case of the spring wood tracheids there is a considerable difference in the averages for the 3 major habitats. There is a discernible increase in the size of the tracheids with increase in distance from the pith. There is also some indication of a decrease in size with increased age of the trees (Table I). The significant fact, however, is the smaller radial diameter of the tracheids from the lava bed trees (27.4 microns) as contrasted with those from the virgin timber (31.3 microns) and especially with those from the sphagnum bog trees (37.0 microns) (Fig. 7). The 6 minor habitats

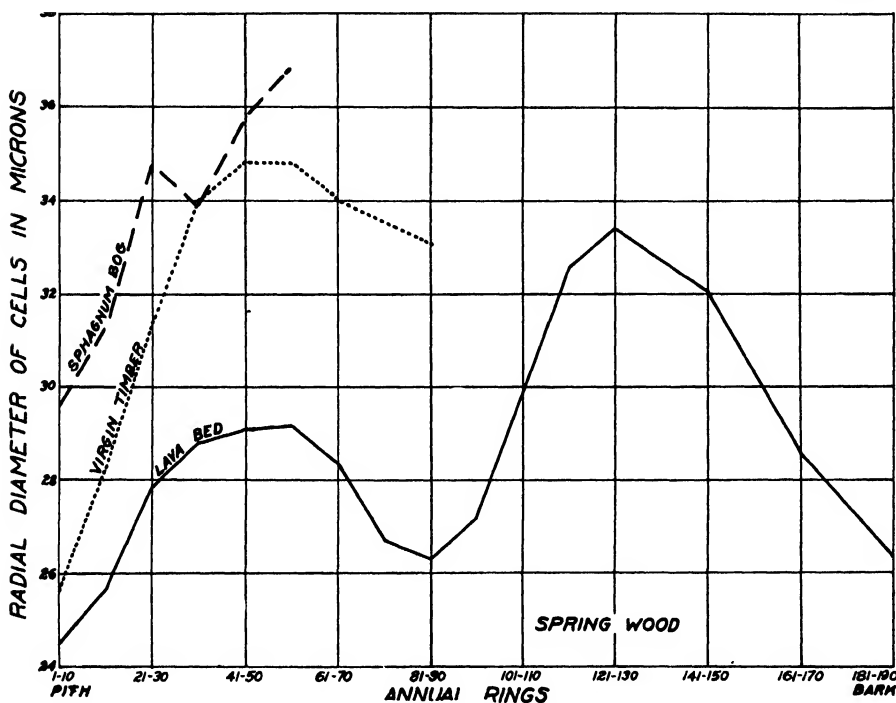


FIG. 7. Radial diameter of the spring wood tracheids expressed in microns. Average of measurements of all trees from the sphagnum bog, virgin timber, and lava bed habitats, respectively. Curves smoothed by the 3-point moving average method.

arranged themselves in a slightly different order from that of per cent of summer wood, namely; mixed forest, lava blocks forest, lodgepole pine forest, open second growth forest, dense virgin timber forest and sphagnum bog forest. The size of the tracheids from the 3 lava bed forest types remains rather uniform from the pith to the bark or shows a decrease near the bark, whereas the tracheids of the virgin timber and sphagnum bog forest types show a distinct increase in size from pith to bark. This may be due to more severe environmental factors and consequently early ageing of the trees on the lava bed. In comparison, the open second growth forest type shows a

very rapid increase. These trees are all young, not over 80 years, and are growing in the open with very little competition.

SUMMER WOOD TRACHEIDS

The summer wood tracheids from the three major habitat trees show distinct differences in size (Table I). Comparing the first 60 rings, we find the tracheids from the lava bed trees to be the smallest (16.9 microns) with the virgin timber next larger (19.4 microns) and those from the sphagnum bog trees largest (23.3 microns) (Fig. 8). No distinct upward trend

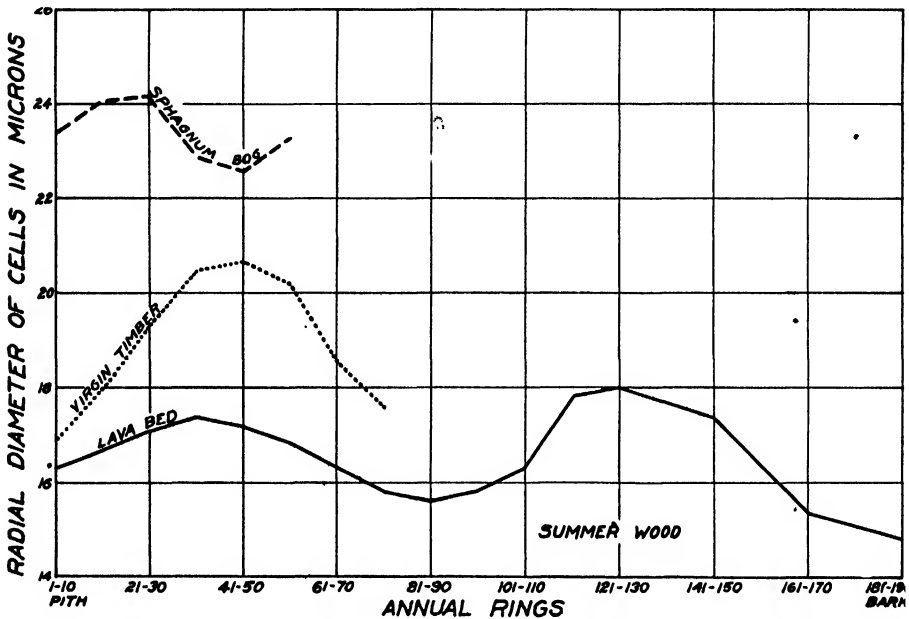


FIG. 8. Radial diameter of the summer wood tracheids expressed in microns. Average of measurements of all trees from the sphagnum bog, virgin timber, and lava bed habitats, respectively. Curves smoothed by the 3-point moving average method.

is noticeable with the exception of the open second growth forest tracheids. The 6 minor habitats are arranged in the same order as that for spring wood tracheids.

TANGENTIAL DIAMETER OF THE TRACHEIDS

The number of tracheids covering 530 microns in a tangential direction was counted in every fifth ring and their average size calculated. Only the tracheids of the summer wood were measured, since no significant difference in tangential size between summer and spring wood tracheids was noted.

The differences in tangential diameter of the tracheids are not as great as the differences in radial diameter (Fig. 9). This is in conformity with results obtained in a similar study on mountain hemlock (Kienholz, '30).

The 3 major habitats are arranged in the same order, however. The average of the first 60 rings shows that the tracheids from the lava bed trees have the smallest tangential diameter (24.0 microns), the virgin timber next larger (25.2 microns) and those from the sphagnum bog trees largest (27.3 microns) (Table I). The 6 minor habitats are arranged in the same order as

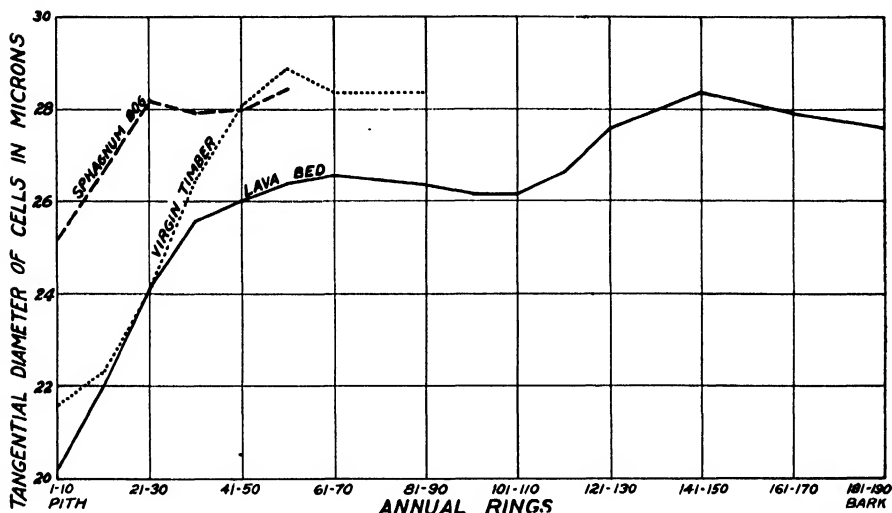


FIG. 9. Tangential diameter of the summer wood tracheids expressed in microns. Average of measurements of all trees from the sphagnum bog, virgin timber, and lava bed habitats, respectively. Curves smoothed by the 3-point moving average method.

they are for the radial diameter of both spring and summer wood tracheids. A distinct upward trend is discernible in all of the curves, showing an increase in tangential size of the tracheids from the pith to the bark.

THICKNESS OF TRACHEID WALLS

The thickness of the walls of occasional spring and summer wood tracheids was measured under a higher magnification of the microscope, and the results show a slight increase in thickness from the lava bed trees with spring wood tracheid walls 5.97 microns and summer wood tracheid walls 13.17 microns in thickness, to the sphagnum bog trees with spring wood tracheid walls 7.35 microns and summer wood tracheid walls 14.21 microns in thickness. The data are not sufficient in amount to differentiate between the different minor habitats. The greater thickness of the tracheid walls from sphagnum bog trees, when compared with lava bed trees, can be determined merely by casual observation. The spring wood tracheids of the first 5 or 10 annual rings near the pith usually have walls nearly as thick as those of the summer wood tracheids; but further from the pith the differentiation between spring and summer wood becomes sharp.

LENGTH OF TRACHEIDS

Every 10th, or in some cases, every 20th ring from the pith to the bark was examined in determining the length of the tracheids. Thus the 1, 11, 21, etc., rings from the pith to the bark at the 2 foot level, and in a few cases also at higher levels, were macerated and the length of the tracheids measured. In every case an entire ring was taken, or if the rings were narrow, 2 entire rings were taken so as to equalize any possible differences in the length of the tracheids from spring and summer wood. Investigators differ on this point, some maintaining that spring wood tracheids are longer (Gerry, '15) and others that summer wood tracheids are longer (Kribs, '16, Lee and Smith, '16). The point was not investigated in this study.

The desired ring was carefully split out into toothpick-like slivers and stored in labeled test tubes. Some hours before using they were soaked in water with or without a few drops of nitric acid. They were then heated to boiling in a solution of about half water and half concentrated nitric acid until they began to disintegrate slightly. Then a large quantity of potassium chlorate was added. Violent chemical action then took place and care had to be exercised to avoid the loss of the "cook." This boiling tended in itself to help separate the tracheids, and, after allowing the chlorate to act a short time, the contents of the test tube were poured into a beaker of water. Experience is the best teacher in learning this process of maceration, as it varies with variation in the amount of each chemical used. It was found also that the different woods varied to some extent in the ease with which a satisfactory maceration was obtained, sphagnum bog wood macerating more easily but the tracheids being frequently broken because of their great length. The wood nearest the pith was apparently the most difficult to macerate satisfactorily.

The mass of tracheids in the beaker was very thoroughly stirred before each mount was made, to insure adequate random sampling. The tracheids were withdrawn with a medicine dropper and mounted in water on a slide. One hundred tracheids were measured from each ring examined. This required the making of several mounts. Care was taken not to measure any tracheid twice. No selection was exercised in the measuring of the tracheids beyond avoiding those which were broken. A low power objective and a calibrated ocular micrometer were used.

The following discussion is based on the averages of the measurement of over 17,000 tracheids from the 18 trees growing in the 3 major habitats (6 minor habitat divisions) already discussed.

The average of all tracheids measured at the 2 foot level is 2.42 mm. The longest single tracheid measured is 5.67 mm., the shortest 0.33 mm. long (Table III).

The maximum average tracheid length for a single annual ring is 4.30 mm. for the 121st ring of tree No. 8 in the lodgepole pine forest on the lava bed,

TABLE III. *Length of tracheids in millimeters*

Average of measurements of all trees from the sphagnum bog, virgin timber and lava bed habitats at the 2 foot level, based on the measurement of 13,200 tracheids.

Ring number, pith to bark	Lava bed	Virgin timber	Sphagnum bog
1	0.78	0.82	0.86
11	1.52	1.49	1.90
21	1.91	2.04	2.45
31	2.21	2.38	2.69
41	2.49	2.71	2.78
51	2.68	2.88	2.85
61	2.83	3.06	
71		3.47	
81	3.12	3.50	
91	3.40	3.88	
101	3.23	3.66	
111	3.50		
121	3.43		
131			
141	3.82		
151	3.86		

whereas the minimum average tracheid length for a single annual ring is 0.65 mm. in the first ring of tree No. 4 found in the lava blocks forest.

In every case at the 2 foot level the tracheids near the pith are short (Ave. 0.81 mm.) but increase in length very rapidly toward the bark (Fig. 10). This increase becomes more gradual until the tracheids reach a maximum length, after which they fluctuate above and below a certain average. The age at which this maximum is reached seems to vary in different trees. In most of the trees examined, the tracheids apparently had not reached a maximum length, as the general slope of the curve representing the length of the tracheids was still upward. Thus in the case of tree No. 49 from the mixed forest at the edge of the lava bed, the tracheids were still increasing in length at the 151st ring, whereas one of the lava blocks forest trees showed a falling off after 41 years. If a greater number of much older trees had been used it might have been possible to determine at what age the maximum was reached in each habitat. It is likely that the age at which this maximum was reached would vary with the different habitats. It would probably be reached earlier in habitats such as the lava blocks forest where conditions are severe, or in the virgin timber where competition with other trees is very keen, whereas in the open second growth forest it would be reached later. In most of the habitats such trees were not available, or, if available, did not represent the average condition of the trees in that habitat. In the data at hand practically all of the curves of tracheid length show a distinct flattening as they approach the bark, indicating that the maximum length has very nearly been reached.

The 6 minor habitats arrange themselves in the usual order except that

the tracheids of the 3 open second growth forest trees are unusually short, differing little from those from the lodgepole and mixed forests. The difference in length of the tracheids from the different habitats is not very great, as can be seen from Table III, but they arrange themselves in the order of increasing length as follows: mixed forest, open second growth forest,

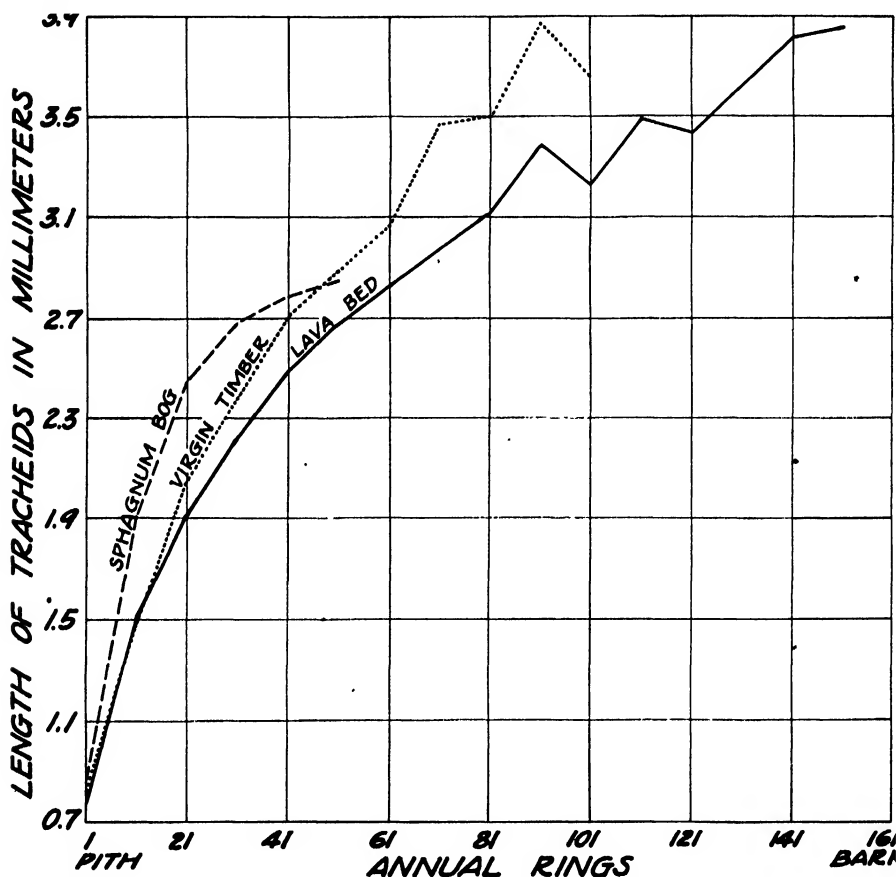


FIG. 10. Length of the tracheids expressed in millimeters. Average of measurements of all trees from the sphagnum bog, virgin timber, and lava bed habitats, respectively, at the 2 foot level. (Based on the measurements of 13,200 tracheids.)

lodgepole pine forest, lava blocks forest, dense virgin timber forest and sphagnum bog forest.

The 3 major habitats show slight differences in tracheid length when compared with each other (Fig. 10). The lava bed trees have the shortest tracheids, the sphagnum bog trees the longest, and those from the virgin timber trees are intermediate. The difference in length is least near the pith (0.19 mm.), and the increase in length is subject to little fluctuation; in other words, the curves are straight. Further from the pith the individual

curves fluctuate more widely and they likewise diverge more widely from each other (0.62 mm. at the 61st ring). Apparently the length of the tracheids does not vary as widely nor as directly in response to different environmental conditions as does the radial diameter of the tracheids.

Tracheid length was also determined for every tenth ring at higher levels in 2 trees, one from the open second growth forest and one from the sphagnum bog forest. There is a distinct increase in the length of the tracheids from the pith to the bark at every higher level 12, 22, 32, 42, and 52 feet as well as at the 2 foot level. There is also a distinct increase in length of the tracheids in a given annual ring from the base of the tree upward with some indication of a falling off as the extreme top is reached. This increase is least near the pith and greatest near the bark (Fig. 11); and is fairly con-

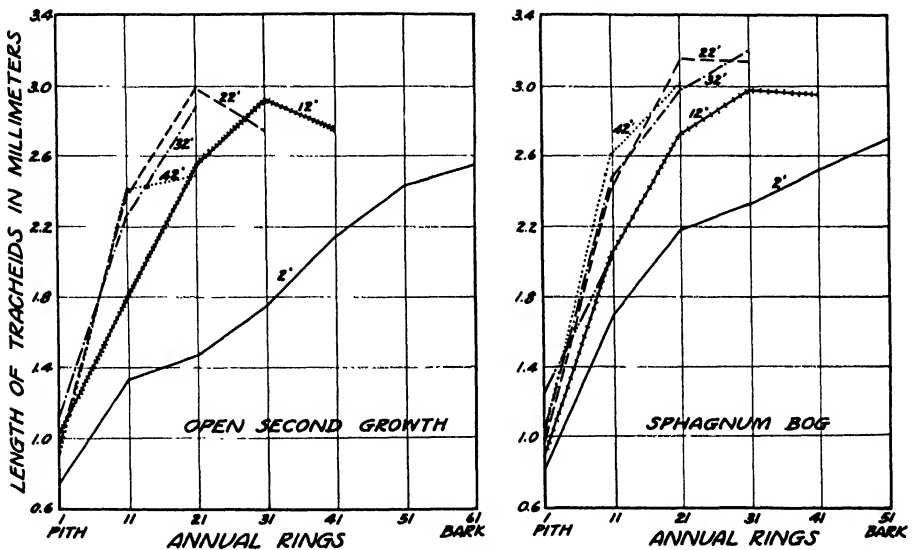


FIG. 11. Length of the tracheids expressed in millimeters. Average of the measurements of one tree from the open second growth forest and one from the sphagnum bog forest at the 2, 12, 22, 32, 42 and 52 foot levels. (Based on the measurement of 4,600 tracheids.)

stant. Only at the highest levels and near the bark is there apt to be any crossing of the curves. There seems to be no significant difference in the tracheid lengths at higher levels in the sphagnum bog forest tree as compared with the open second growth forest tree, except that in general all of the tracheid lengths are a little greater in the case of the sphagnum bog tree.

When we examine the figures for the individual trees we find that a tree in a given habitat which grows very rapidly in height has wider annual rings, larger tracheids (radial and tangential diameter) and longer tracheids than another tree from the same habitat which is not so tall for its age. But the per cent of summer wood is less in the tall tree than in the slower growing

ones. This is particularly evident in the case of tree number 8 which is very tall for its age as compared with trees 12, 25, 27 and 32. The same applies for tree number 81 as compared to trees 82 and 83. This seems to bear out the contention that height is an accurate index of not only quality of site, as is held by many foresters, but also of individual vigor of growth in a supposedly uniform habitat. This assumption is worthy of closer investigation.

SUMMARY

1. The wood structure of 18 lodgepole pine trees (*Pinus contorta*) from 6 different habitats was examined. The 6 habitats were divided into 3 groups with major habitat differences between them. These major habitats are: (1) lava bed, (2) virgin timber, and (3) sphagnum bog, all located in or to the west of the Cascade Mountains, Washington.

2. The trees were all cut at the 2 foot level and wood along the average radius was used for the study.

3. The lava bed trees grew under conditions of shallow, poor soil, probably insufficient water at certain seasons, high evaporation rates, strong insolation, and very great diurnal temperature fluctuations.

4. The virgin timber trees grew under conditions of deep but not rich soil, adequate water, low evaporation rates, slight temperature fluctuations, and greater competition with surrounding trees.

5. The sphagnum bog trees grew in a substratum of sphagnum, with decided diurnal temperature fluctuations and great differences in temperature of air and soil, low evaporation rates, abundant but probably somewhat toxic water.

6. In growth rate (width of annual rings) the lava bed trees are slowest (1.87 mm. of diameter added per year), sphagnum bog trees most rapid (4.02 mm.) with virgin timber intermediate (3.80 mm.). This is an unusually high growth rate for sphagnum bog trees, however.

7. The per cent of summer wood per annual ring shows the same relationship, with the lava bed trees having the least summer wood (22 per cent), sphagnum bog trees the most (44.7 per cent), and virgin timber trees intermediate (28.5 per cent).

8. The increase in width of the rings is due in part to increase in the radial diameter of the tracheids, but more in the number of tracheids laid down. The rings from sphagnum bog trees average 68.5 tracheids in width, virgin timber 50.0, and lava bed 39.0.

9. The radial diameter of the tracheids is least in the lava bed trees (spring 27.4 μ , summer 16.9 μ), greatest in the sphagnum bog trees (spring 37.0 μ , summer 23.3 μ), and intermediate in the virgin timber trees (spring 31.3 μ , summer 19.4 μ).

10. The same order holds for the tangential diameter of the summer wood tracheids though without as pronounced differences (lava 24.0 μ , sphagnum 27.3 μ , virgin timber 25.2 μ).

11. The thinnest tracheid walls were found in the wood of the lava bed trees (spring $5.97\ \mu$, summer $13.17\ \mu$), the thickest in the wood of the sphagnum bog trees (spring $7.35\ \mu$, summer $14.21\ \mu$).

12. The wood of every 10th or 20th ring from the pith to the bark was macerated and the length of 100 tracheids measured from each.

13. The average length of all tracheids measured (17,800) was 2.42 mm., the absolute maximum 5.67 mm., the absolute minimum 0.33 mm.

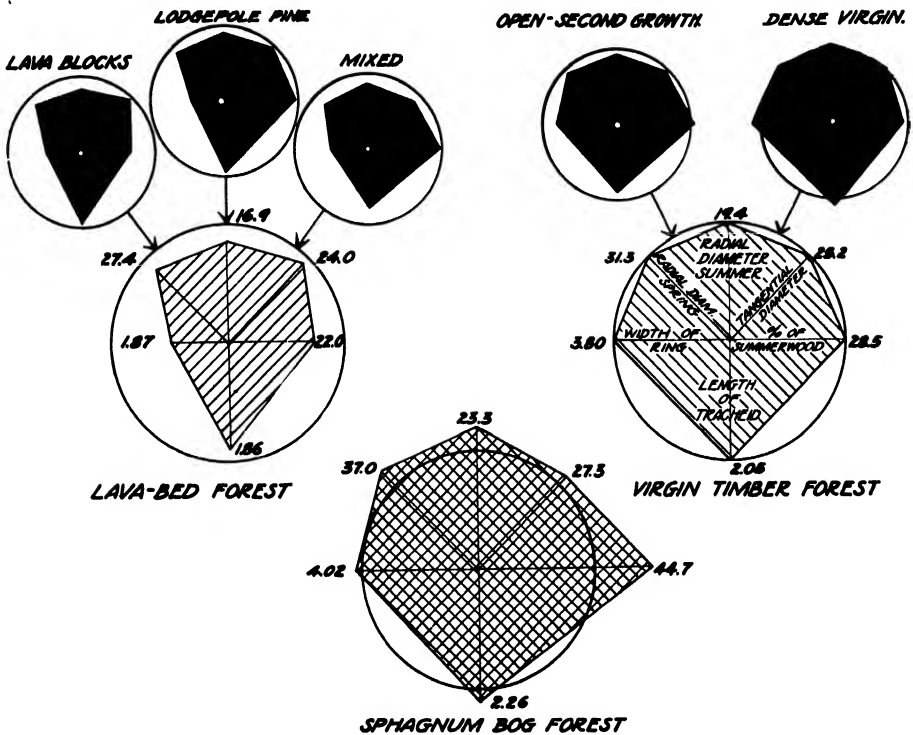


FIG. 12. Summary of all measurements on all trees from the 6 minor habitats and the 3 major habitats. Each measurement expressed on a radius in proportion to the virgin timber measurement considered as unity (i.e., 100). Actual figures given are: millimeters—length of tracheid and width of ring; microns—radial and tangential diameters, and per cent of summer wood.

14. The length of the tracheids increased from the pith to the bark, at first very rapidly and then more slowly.

15. There was a slight difference in length in favor of the sphagnum bog trees. The lava bed trees had the shortest tracheids, with the virgin timber intermediate.

16. There was a distinct increase in length from the base toward the top of the tree. This increase was about the same for the trees in the different habitats.

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EFFECTS OF 1925 SUMMER DROUGHT ON SOUTHERN APPALACHIAN HARDWOODS

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METEOROLOGICAL OBSERVATIONS

A drought of extraordinary severity occurred in the Southern Appalachian region during the summer of 1925. The rainfall, as reported by the U. S. Weather Bureau Station at Asheville, North Carolina, was as follows: May, 2.15 inches; June, 1.97; July, 0.77; and August, 0.22. The normal average for the Asheville station, based on 27 years' records, is, for May, 3.49 inches; June, 3.97; July, 4.47; and August, 4.04. For the 4 months considered, the total rainfall in 1925 was thus 5.11 inches, or

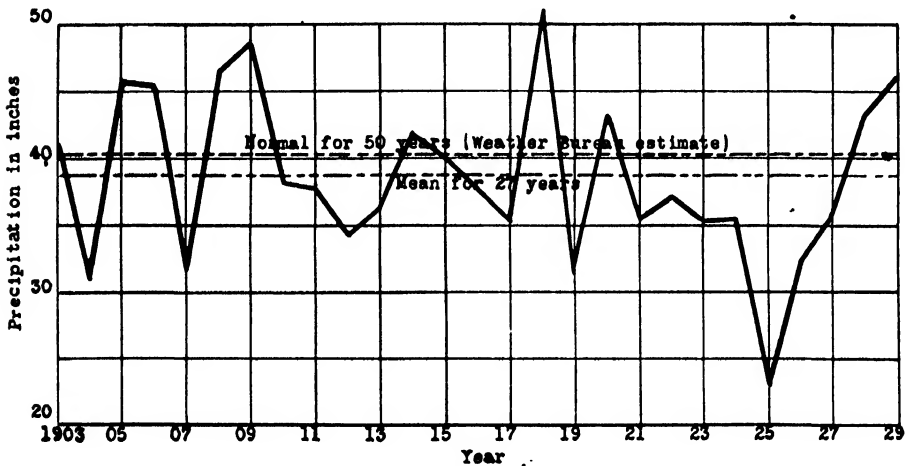


FIG. 1. Annual precipitation for the period 1903-1929, Asheville, North Carolina.

about 32 per cent of the mean normal summer rainfall of 15.97 inches. For July and August it was only 11.6 per cent of the normal average.

Annual precipitation² throughout the 27-year period, 1903-1929, is shown in figure 1. It is to be observed that considerable annual fluctuation from the normal occurs, precipitation ranging from a minimum of 22.79 to a maximum of 51.08 inches. Figure 2 shows the total summer precipitation,

¹ Formerly Appalachian Forest Experiment Station.

² These data are taken from the reports of the U. S. Weather Bureau Station at Asheville, North Carolina.

ranging from a minimum of 2.96 to a maximum of 19.27 inches, for the period 1903-1929.

BEHAVIOR OF THE FOREST

During August and September of 1925 the leaves of many trees on ridges and upper slopes of the Bent Creek Experimental Forest, 10 miles from Asheville, became wholly or partially brown, and some species fell prematurely. This forest lies at an altitude of 2,100 to 2,600 feet, and is composed chiefly

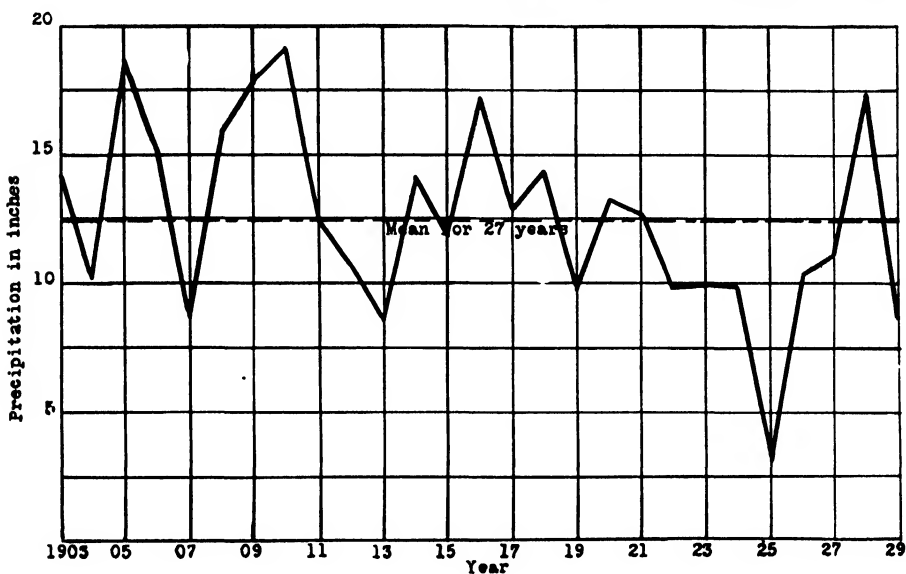


FIG. 2. Summer precipitation (June, July, August) for the period 1903-1929, Asheville, North Carolina.

of oaks, short-leaf and pitch pines (*Pinus cchinata* Mill. and *P. rigida* Mill.). In September, two small areas conspicuously affected by the drought were placed under close observation. One was located on an upper west slope, the other on a middle east slope of one of the low forested mountain ridges.

Observations were made of tree conditions, topography, and soil. Individual trees were tagged and described as to bole condition, crown, vigor, dominance, and leaf injury by drought. The leaf browning and early leaf fall were more pronounced among the younger trees. The browning appeared to be particularly severe on dogwood (*Cornus florida* L.), sourwood (*Oxydendrum arboreum* (L.) DC.), and chestnut (*Castanea dentata* (Marsh.) Borkh.), while white ash (*Fraxinus americana* L.), black locust (*Robinia pseudoacacia* L.) and pignut hickory (*Hicoria glabra* (Mill.) Sweet), showed less injury from the drought. Trees with large logging or fire scars showed more severe browning of the leaves than those with sound boles. On many of the large trees, the browning was confined to the top-most branches.

SOIL MOISTURE

The soil on the area under observation was relatively shallow, being seldom more than 18 or 20 inches in depth. It is mapped by the U. S. Soil Survey as Porter's stony loam and Porter's clay loam. Over much of the area showing severe drought injury the bed rock is close to the surface, with frequent rock outcrops. The topography is steep, the degree of slope ranging from 50 to 100 per cent.

Determinations of moisture content of the soil at the time of the drought and in the year following, disclosed wide differences. In September, 1925, there was an average of from 5 to 6 per cent moisture, oven-dry basis, for the 4 inches of surface soil, and of 8 to 11 per cent at a depth of 1 foot. In the early summer of 1926 the moisture content had increased to a range of from 15 to 40 per cent oven-dry basis. In some locations where rock outcrops were abundant the shallow soil was found to have a moisture content of from 40 to 45 per cent, as compared with 5 per cent at the time of the previous sampling during drought conditions. No study was made of available moisture of the soil, but considering the amount of clay present, it is reasonable to believe that when reduced to a moisture content of 5 per cent this soil has no water available to the plant roots.

SUBSEQUENT RESULTS

The condition of the trees was again recorded in September, 1927, and in September, 1929. An insufficient number of individuals of each species was under observation to permit an analysis of the data on a statistical basis; nevertheless certain outstanding facts may be considered as significant. During the succeeding 4 years not one of the tagged trees that maintained normal foliage during the drought period showed any evidence of injury that could be attributed to the drought. About half of the trees showing definite drought injury at the time of tagging in September, 1925, completely recovered. The remainder sustained injury in the form of dead branches in the crown, or were killed by drought or by secondary causes.

BEHAVIOR OF SPECIES

Considerable differences in response to the drought were shown by the several species under observation. The leaves of the dogwood turned brown at the distal end, the rest of the leaf retaining its green color; those of the basswood, ash, and hickory were lost prematurely.

In other species—oaks, for example—the leaves that turned brown became completely so, although other leaves on the tree remained green. The leaves of the chestnut oak (*Quercus montana* Willd.) were only moderately or slightly injured; the trees were quite normal the following spring, and no permanent injury could be attributed directly to the drought. Black oak (*Q. velutina* Lam.), showed severe leaf injury during the drought period and all

of the trees of this species were dead in 1929. With few exceptions, red oak (*Q. borealis* Michx.) and scarlet oak (*Q. coccinea* Muenchh.) responded similarly to black oak. The hickory species present, mockernut (*Hicoria alba* (L.) Britt.), pignut (*H. glabra* (Mill.) Sweet), and shagbark (*H. ovata* (Mill.) Britt.), were only slightly injured during the drought, the principal response being an early shedding of the leaves. In most cases recovery among hickories was complete.

Increment borer cores of the trees that recovered completely after the drought season showed that there had been little appreciable reduction in annual diameter increment either in the drought season or during the following years. Those trees, however, which died during the 4 years succeeding the drought showed a definite reduction in diameter increment for the years in which they remained alive after the dry season.

DISCUSSION

Extensive root excavations were impracticable because of rock obstructions, but it seemed likely that root restriction due to rock outcrops or to shallow soil rock pockets was the significant factor responsible for the drought injury. A similar conclusion was reached by Meinecke³ as a result of a study of drought injury to forest trees in the Sierra Nevada Mountains of California. On the Bent Creek area the greatest drought injury occurred in the case of trees with restricted root systems growing on shallow soil, which explains differences in reaction between individuals of the same species. This fact alone, however, would not account for the differences in behavior of various species, a phenomenon that can be properly explained only after we shall have obtained, through adequate research, an increased knowledge of root development and hydrostatic systems of various tree species.

An increased mortality among scarlet, black, and red oaks in the Southern Appalachians has been recorded for the year 1927 by Balch.⁴ While he does not ascribe the increased mortality to a definite primary cause, severe late frosts in April, 1927, which completely killed the new foliage over much of the Bent Creek region, no doubt lowered the vitality of the trees. The general conclusion is that a combination of unfavorable seasonal conditions reduced the vigor of the individual trees already of low vitality due to overmaturity or competition; subsequently the shoestring fungus (*Armillaria mellea* (Vahl) Quel.), together with certain insects, particularly the two-lined chestnut borer (*Agrilus bilineatus* Web.) and certain species of *Prionus*, the long-horned beetles, or a combination of these parasites, brought about the death of the trees. During the spring of 1929 many trees of scarlet oak were wind-thrown throughout the region in the vicinity of Ashe-

³ Meinecke, E. P. An effect of drought in the forests of the Sierra Nevada. *Phytopathology*, 15: 549-553, 1925.

⁴ Balch, R. E. Dying oaks in the Southern Appalachians. *Forest Worker*, 3: No. 6, p. 13, 1927.

ville. The shoestring fungus was associated with the roots of all such wind-thrown trees as were examined. The prevalence of this root fungus may also be the result of irregular seasonal precipitation and the late spring frost that occurred in the 4 years preceding 1929. It is possible that these climatic conditions disturbed the natural resistance of the tree against its parasitic enemies.

As a rule, ground water follows the rock formations on mountain slopes, and rock outcrops often give rise to moist areas where the extent and vigor of the vegetative growth is out of proportion to the amount of soil present. During periods of drought this ground water is absent, and the shallow soil becomes dried down to the bed rock, causing injury to the relatively luxuriant vegetation. This injury frequently results in the death of annual plants. Herbaceous perennials die down to the ground, but their roots remain alive unless the drought is unusually severe. Small woody plants, such as alder (*Alnus* sp.), may also die to the ground but may sprout up from the roots the following year when moisture conditions become adequate.

The varied reactions observed in 1925 in the case of the tree species have already been described. It is obvious that these various adaptations, the partial or complete browning of the leaves and the premature leaf fall, result in a reduction of the transpiring area. Those species, therefore, whose individuals are able to respond in this way to drought conditions are better fitted, from this standpoint, for situations subject to occasional summer dry periods.

It is believed that during excessively dry seasons, drought injury similar to that of 1925 has occasionally occurred in the past in the Southern Appalachian Mountain region, and has constituted an important factor in determining the composition of the natural forest stands. Because of the fluctuations in annual precipitation in the region the same sort of injury is to be expected in the future. Drought conditions in the Southern Appalachians favor the occurrence of forest fires during the summer. These forest fires also have been influential in determining the nature and composition of the mountain forests.

It is frequently stated by writers on general forestry that the climate of the Southern Appalachians is favorable to the growth of a heavy deciduous forest. No attempt will be made to discuss this general statement in the present paper. Observations on the 1925 drought, however, suggest that wide fluctuation from the normal means in seasonal precipitation are of salient significance in the distribution of tree species growing in regions of irregular topography. It is suggested that the minimum of the fluctuating precipitation range must be considered in determining the site possibilities for any given tree species. If this is true, many of the tree species now present in the stands of the ridge and upper slope forest in the Southern Appalachians are relatively unproductive.

Those tree species that are injured but not killed in dry years will remain in and become a menace to the vigor of the stand, exhibiting poor form, stag-



FIG. 3. Drought-injured forest on upper slope, Bent Creek Experimental Forest, near Asheville, North Carolina. Photograph by the Appalachian Forest Experiment Station, U. S. Forest Service, March 20, 1930.

headedness, and slow growth. Where fire has accompanied the drought the poor vigor of the crippled trees is even more marked. It is probable that these factors account for many of the crippled hardwoods that control the upper slopes and ridges (Fig. 3) many of these species are obviously out of their favorable habitat, and yet through their unusual persistence under unfavorable circumstances they continue to hinder the establishment of other tree species possibly more suited to the dry slope and ridge conditions.

Efficient utilization of the upper slopes and ridges in the Southern Appalachians for watershed protection is a problem of much concern. Observations on seasonal droughts have a practical application to this problem. The minimum seasonal precipitation appears to be a critical factor in determining the growth of tree species on the upper mountain slopes. Due consideration must be given to this fact in the choice of tree species to be selected in any planting program, or favored in any management plan, for the upper slopes and ridges of the Southern Appalachian Mountains.

SUMMARY

For the year 1925 the annual precipitation in the Southern Appalachian region was approximately one-half of the annual mean for 27 years. The summer precipitation (June, July, August) was less than one-fourth of the summer mean.

The precipitation deficiency expressed itself on the vegetation of the region through early browning and premature leaf fall.

Most of the trees on good sites apparently recovered completely the following year. On upper slopes and on shallow or rocky soils some tree species that had established themselves during cycles of sufficient precipitation were severely injured or killed, either directly or subsequently through secondary agencies.

Partially killed crowns, resulting in stagheaded trees, were of common occurrence on shallow soils. Black oak (*Quercus velutina* Lam.) was particularly susceptible to the drought. Chestnut oak and pine survived on areas where black oaks were completely killed.

Precipitation records indicate a considerable annual and seasonal fluctuation for the Southern Appalachian region. Drought conditions have occurred in the past and may be expected in the future. This fact should be considered in determining certain forestry practices in the Southern Appalachians, particularly in regard to planting of species on the upper slopes where drought conditions may become severe.

STUDIES IN ARTHROPOD HIBERNATION. III. TEMPERATURES IN FOREST HIBERNACULA¹

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During a field study of arthropods of forest environments in the Chicago region covering a period of 3 winters, a great variation in hibernaculum conditions and winter habitat selection was noted. Some species were found in old insect burrows deep in old, much-decayed logs, oftentimes surrounded by frost crystals and even ice, while other species were found consistently in the more exposed places under very loose, dry bark of standing dead trees. Some species selected recently-felled trees, others very much decayed logs. Leaves sheltered a very large number of species. Decaying grass, old plant stems, and the soil itself offer shelter to a host of arthropods. In these field studies, it was observed that moisture played a large part in this selection, and it was assumed that amount of protection against the low temperatures of winter was likewise a determining factor. Only a few scattered determinations of temperatures in particular hibernacula were made in the field. The temperatures that were determined, whether with thermometers or thermocouples, indicated that there was often a considerable difference between the hibernaculum and the air temperatures. Accordingly, the following studies were carried out during the winters of 1924-1925 and 1925-1926 to determine the exact temperatures occurring in a limited number of the commonest, forest hibernacula, viz., in leaves, under bark, and in logs in middle and late stages of decay.

A number of studies of temperature conditions occurring in logs and trees have been made (Harvey, Craighead, Graham, Emerson, Mix and others), but to the best of the author's knowledge, these have been made with a different purpose or at a different season of the year.

THERMOGRAPH RECORDS

Continuous thermograph records of hibernaculum temperatures were kept from November, 1924, to the end of the following April. Three thermographs were first thoroughly tested and regulated. The bulb of one was then placed in about 2 bushels of oak leaves which had been spread out on the ground over an area of $2\frac{1}{2}$ by $2\frac{1}{2}$ feet. There were about 2 or 3 inches of loose leaves above and below the bulb. A medium-mesh chicken wire, resting lightly on top of the leaves, prevented their disturbance by wind and animals.

¹ This work was done at Whitman Laboratory, University of Chicago, under the direction of Dr. W. C. Allee.

An attempt was made to simulate natural conditions as much as possible. At the time of beginning the experiment, the leaves had been slightly moistened by a rain during the previous night. During the experiment, they were fully exposed to sun, wind and precipitation.

The bulb of the second thermograph was placed under the bark of a large piece of old basswood (*Tilia americana*) log, $4\frac{1}{2}$ feet long, $1\frac{1}{2}$ feet wide. The tree from which this piece came must have been between 2 and 3 feet in diameter. A large piece of bark, $\frac{1}{2}$ to 1 inch thick, covered one side. The wood underneath was in the last stage of decay—soft and full of old insect burrows. The large piece of bark was removed intact, a cavity was hollowed out in the surface wood just large enough to accommodate the thermograph bulb, and the large piece of bark again replaced over the bulb. Three or four nails were driven through the bark into the wood to hold the bark in place, but the wood was so soft that the nails did not tightly bind the bark. This piece of log was the kind in which one would expect to find a large number of hibernating arthropods during the winter, such as tipulid larvae, *Pyrellia serena* (Muscidae), *Amblyteles* (Ichneumonidae), etc. When the bark was removed, the log was found to contain cerambycid larvae. This log was placed beside the leaves.

Both leaves and log hibernacula simulated forest habitats, except that they were in the open, and hence more exposed to temperature extremes than if they had been in a forest.

To secure the air temperature record, the bulb of the third thermograph was suspended with the lower end of the bulb 6 inches above the leaves and logs. A shallow box, open on the under side, was placed over it to serve as a protection against rain and snow. It was therefore shaded throughout the experiment.

The three recording instruments were placed on a shelf in a greenhouse 4 or 5 feet away.

The winters in the Chicago area show great variation. Some winters have relatively little snow fall; in other years, there may be a snow covering throughout the winter. The weather conditions during the winter of 1924–1925 were unusually fortunate. A rain, beginning on December 16, turned into sleet the following day, thus coating the experimental log and leaves with a thick layer of ice, which remained the entire winter. On December 18, the first snow fall occurred. Snow covered the ground until February 7, part of the time to a depth of 5 inches. The experimental hibernacula were therefore sealed and insulated with snow and ice during the entire winter. The temperature conditions in the hibernacula were unusually favorable for the experiment as well as for insect life, as the following data will show.

During the course of the experiment, the thermographs were all checked by means of thermometers and thermocouples. It was found that the thermographs recording temperatures in air and leaves were registering satisfactorily. The thermograph in the log, however, registered 6.42° – 8.89° C. (av-

erage 7.6°C.) higher than the thermocouple readings, for some unaccountable reason. In the following data (Fig. 1), I have taken the liberty of lowering the recorded temperatures for this thermograph 7.6°C. on the basis of the above check and because of results obtained the following winter.

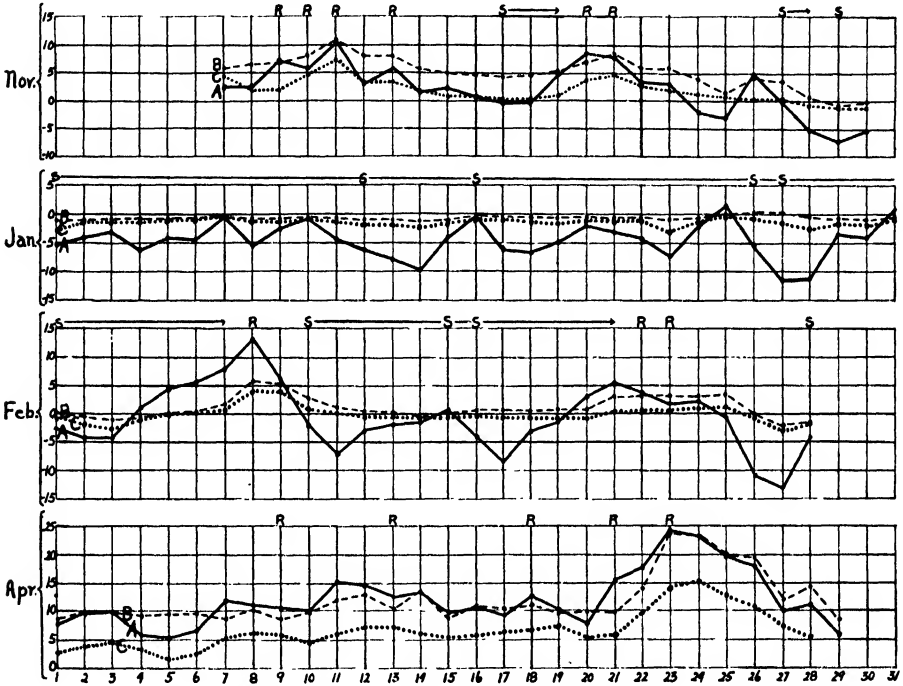


FIG. 1. Mean daily temperatures in hibernacula during fall, winter and spring (thermograph determinations). Graph A = air temperatures; graph B = temperatures in leaves; graph C = temperatures under bark of log in late stage of decay. S = snow fall; R = rain. Duration of snow covering is shown by a line above the graphs. The temperatures in the log have been reduced 7.6°C. from the actual thermograph record as explained in the text.

The data obtained are presented in figure 1. The points in the graph represent mean daily temperatures which are shown on the ordinates against the days of the month, plotted on the abscissae. Precipitation is shown by the horizontal line at the top.

It is seen that during the month of November, the mean temperatures of both log and leaves fluctuated readily with the mean air temperatures before freezing occurred, but at the end of the month, when the mean air temperatures went below zero and snow had covered the ground, the mean hibernaculum temperatures stayed around zero. Table I shows that in November, while the air temperatures were fluctuating between the extremes of 17.0° and -11.4°C. , a variation for the month of 28.4°C. , the mean temperatures in the leaves showed an extreme variation of only 15.1°C. and those of the

TABLE I. *Monthly extremes of temperature during the winter of 1924-1925*

	Nov.			Dec.			Jan.		
	Max.	Min.	Var.	Max.	Min.	Var.	Max.	Min.	Var.
Air.....	17.0	-11.4	28.4	12.8	-24.8	37.6	5.9	-16.8	22.7
Leaves.....	13.5	-1.6	15.1	8.7	-5.3	14.0	0.4	-1.5	1.9
Log.....	7.7	-2.2	9.9	6.7	-8.4	15.1	0.0	-3.3	3.3

	Feb.			Mar.			Apr.		
	Max.	Min.	Var.	Max.	Min.	Var.	Max.	Min.	Var.
Air.....	16.8	-17.2	34.0	20.7	-19.6	40.3	32.0	0.4	31.6
Leaves.....	8.3	-3.0	11.3	11.6	-2.0	13.6	34.5	4.3	30.2
Log.....	6.4	-4.9	11.3	10.4	-6.3	16.7	19.0	0.4	18.6

log only 9.9° C. Table II shows that the average daily variation for the month in the hibernacula is considerably less than that of the air, and is about the same in the leaves and log.

December brought the lowest air temperatures of the winter (-24.8° C.). Even with such low temperatures surrounding the hibernacula, the temperature of the leaves descended only to -5.3° C., and that of the log to -8.4° C. (see Table I), while the average daily variation was about a degree less than in November (see Table II). It is significant that even the lowest

TABLE II. *Daily variations in temperature*

	Nov.			Dec.			Jan.		
	Max. Var.	Min. Var.	Aver. Var.	Max. Var.	Min. Var.	Aver. Var.	Max. Var.	Min. Var.	Aver. Var.
Air.....	13.0	1.8	7.3	20.5	1.6	7.8	16.0	1.0	1.0
Leaves.....	5.0	0.3	2.8	4.9	0.0	1.6	0.9	0.1	0.4
Log.....	6.0	0.0	2.1	7.3	0.0	1.7	2.7	0.4	0.97

	Feb.			Mar.			Apr.		
	Max. Var.	Min. Var.	Aver. Var.	Max. Var.	Min. Var.	Aver. Var.	Max. Var.	Min. Var.	Aver. Var.
Air.....	14.6	3.0	7.9	18.4	2.5	10.6	21.7	5.3	12.1
Leaves.....	4.8	0.3	1.6	6.0	0.1	2.9	21.3	2.8	9.3
Log.....	5.0	0.1	1.5	5.1	0.4	2.5	8.0	2.0	4.5

temperatures in the hibernacula were considerably above the under-cooling and freezing points of insects in winter (Bachmetjew, '01; Payne, '26a, '26b).

The temperature conditions of the hibernacula in January were very striking. This was a consistently cold month, the mean air temperatures hovering

at or below zero the entire month (see Fig. 1). While the air temperatures descended as low as -16.8°C. , the lowest temperature recorded for the leaves was only -1.5°C. , and that of the log only -3.3°C. The graphs of figure 1 show an unusually constant temperature in both hibernacula, and the average variation each day was less than a degree.

February was marked by alternate snow, thawing, and rain. The graphs (Fig. 1) show a considerable rise in temperature in the hibernacula as soon as the insulating snow and ice had melted (Feb. 7) and a return to constant temperature at the zero point as soon as snow covered the hibernacula again (Feb. 10). With the snow insulation gone (Feb. 21), the hibernaculum temperatures again descended below zero during the cold wave of that week, but not so much as in December. The average daily fluctuations increased slightly (Table II).

April was characterized by a gradual rise of temperature and no snow. The hibernaculum temperatures during this month followed the fluctuations of the air temperatures closely, just as in November. The maximum temperature recorded in the leaves for the month even exceeded that of the air (Table I). In both air and leaves, the extremes of temperature were much wider, indicating that the leaves afforded little or no temperature protection in the dry condition in which they were at this time. The temperatures in the log rose, but not nearly as much as in the leaves because of the greater amount of moisture in the log.

It may be concluded, therefore, that the hibernaculum temperatures remain remarkably constant when they are frozen and covered with snow. Although the air temperatures may drop far below zero, the hibernaculum temperatures do not descend much below zero, even when the low atmospheric temperatures are continued over a long period. In the fall and spring, however, there is considerable variation in hibernaculum temperatures, but at no time during these observations did the temperatures go below -8.4°C.

THERMOCOUPLE RECORDS

A similar series of temperature determinations in hibernacula was begun in the fall of 1925, using thermocouples instead of thermographs. The thermocouples were constructed of copper and constantan wires, insulated with porcelain insulators and encased in a glass tubing closed at the junction end and sealed at the other end with bee's wax to prevent water from entering the tubing. Readings were taken on a field millivoltmeter (Leeds and Northrup), and translated into centigrade degrees after careful calibration of the couples.

Two logs and a large quantity of leaves were selected for this study. Log I, of black walnut (*Juglans nigra*),² was in the early pulp stage of decay, about 12 inches in diameter and 4 feet long, with loose bark on top ($\frac{1}{4}$ to $\frac{3}{4}$ inch thick). The bark was removed intact from the upper side, and a groove

² Determination by Dr. Geo. D. Fuller and Mr. M. E. Carson.

7½ inches long and wide enough to accommodate the junction and its tubing was hollowed out of the wood. The thermocouple was inserted in this groove, and the bark carefully replaced and tacked down. This junction was intended to give the temperatures in the upper, more exposed parts of this log. A similar junction was inserted in the same way under the bark, but on the lower side of the same log in a well protected place.

Log II was of red oak (*Quercus borealis maxima* (Marshall) Ashe)² in a late stage of decay. This log was also covered with loose bark, and the wood was rather soft, pulpy and discolored. A hole, large enough to accommodate the junction and its glass tubing, was bored into the upper surface of the wood at one end. The hole was 9 inches deep and about ¾ inch below the bark. A similar junction was inserted 5½ inches into the wood of the middle of the log and about 5 inches below the surface, for the purpose of securing the temperatures of the inferior wood.

A large quantity of oak leaves was spread out on the ground beside the logs and covered with a piece of wide-mesh chicken wire to prevent their blowing away. Another junction was inserted 9 inches into the midst of these leaves with a layer of about 4 inches of leaves above and below it.

Another junction was suspended a few inches above the hibernacula in order to secure the air temperatures, and was covered with an inverted tin can to keep the junction dry.

All hibernacula were placed on moist sand, the logs in a north and south direction with the junctions inserted into the north ends. A few leaves were scattered over the surface of the ground around and between the logs so as to simulate natural conditions. All hibernacula were fully exposed to sun and precipitation, but may have been protected from wind to some extent by surrounding buildings, but probably not more so than in their natural location in the woods. The leads from the junctions were run into an adjacent animal house 11 feet from the near ends of the logs. Readings were taken almost daily and on many days several readings at different times of the day from January 19 to May 20, 1926.

The weather conditions during the winter of 1925-1926 were not so constant as those of the previous winter. Thaws and rains alternated with snow falls, so that there was no continuous snow covering over the hibernacula as in the previous winter. Nor were there any severely cold periods.

The results obtained for the month of February are plotted in figure 2. The points in the graphs are actual temperature readings obtained on the various days of the month.

The air temperatures during the entire month hovered around zero, and the hibernacula were frozen during this period. A remarkably constant temperature condition, close to the zero mark, is shown in all hibernacula. The effect of snow insulation is again seen during the period of February 15-19. Two cold waves occurred during this time. The first one came when there was no snow on the ground. The consequent lack of protection



FIG. 2. Daily temperatures in hibernacula during the month of February (thermocouple determinations). A = air temperatures; B = temperatures in leaves; C = temperatures under bark, top surface of black walnut log in middle stage of decay; D = temperatures under bark, lower surface of same log as C; E = temperatures in upper surface wood under bark of red oak log in late stage of decay; F = temperatures in interior of same log as E. S = snow fall; R = rain; circles in graph A = temperatures obtained from records of U. S. Weather Bureau Station on the University of Chicago campus.

caused a marked drop below zero in the hibernacula corresponding to the low atmospheric temperatures. That the hibernaculum temperatures apparently went below the air temperatures is probably due to the fact that lower air temperatures had occurred during the night before the readings were taken, and the hibernacula were showing a lag in adjustment to the rising air temperatures. The second cold wave occurred just after a snow fall that covered the ground, and in consequence the hibernaculum temperatures held their constant zero level. The fluctuating temperature under the upper bark of the walnut log was due to the fact that a crack had occurred in the bark over the thermocouple junction.

The readings for April are shown in a similar manner in figure 3. The first week of the month was characterized by zero weather and a snow blanket which slowly melted away by the tenth of the month. The more exposed surface parts of both logs (C and E) thawed first and began to

show a fluctuating temperature from that date on. The leaves (B) and the more protected parts of the logs (D and F) thawed out more slowly, and by the nineteenth all showed rather wide fluctuations in temperature.

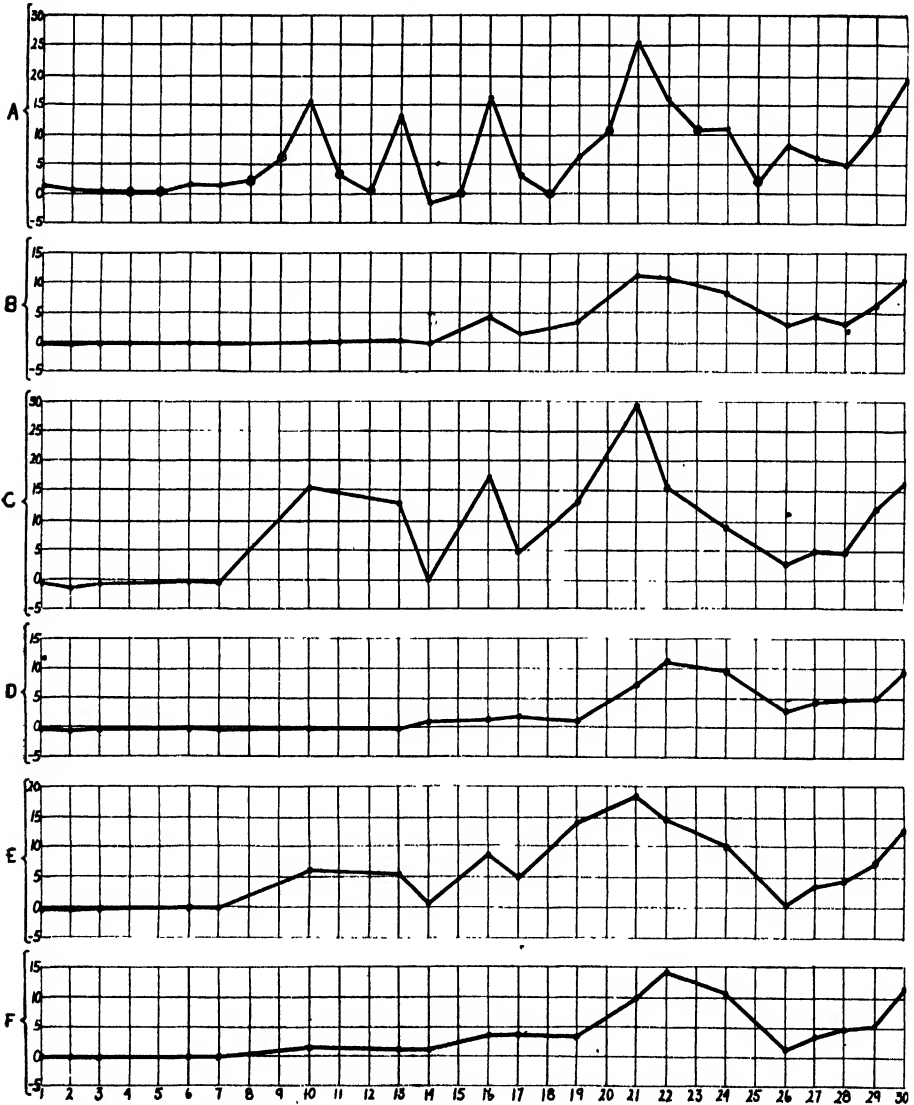


FIG. 3. Daily temperatures in hibernacula during the month of April (thermocouple determinations). Legend as in figure 2.

To determine the daily range of hibernaculum temperatures, several series of 24-hour readings were taken under varying conditions. The same set-up was used for these observations. In fact, the thermocouples and hibernacula were not disturbed. The results of two of these series are shown in figures 4

and 5. The data for figure 4 were obtained on February 18-19 during sub-zero weather, and with the hibernacula covered with at least 3 inches of snow. The graphs show the same constant zero temperatures as described above. The actual ranges of temperatures are shown in Table III. The

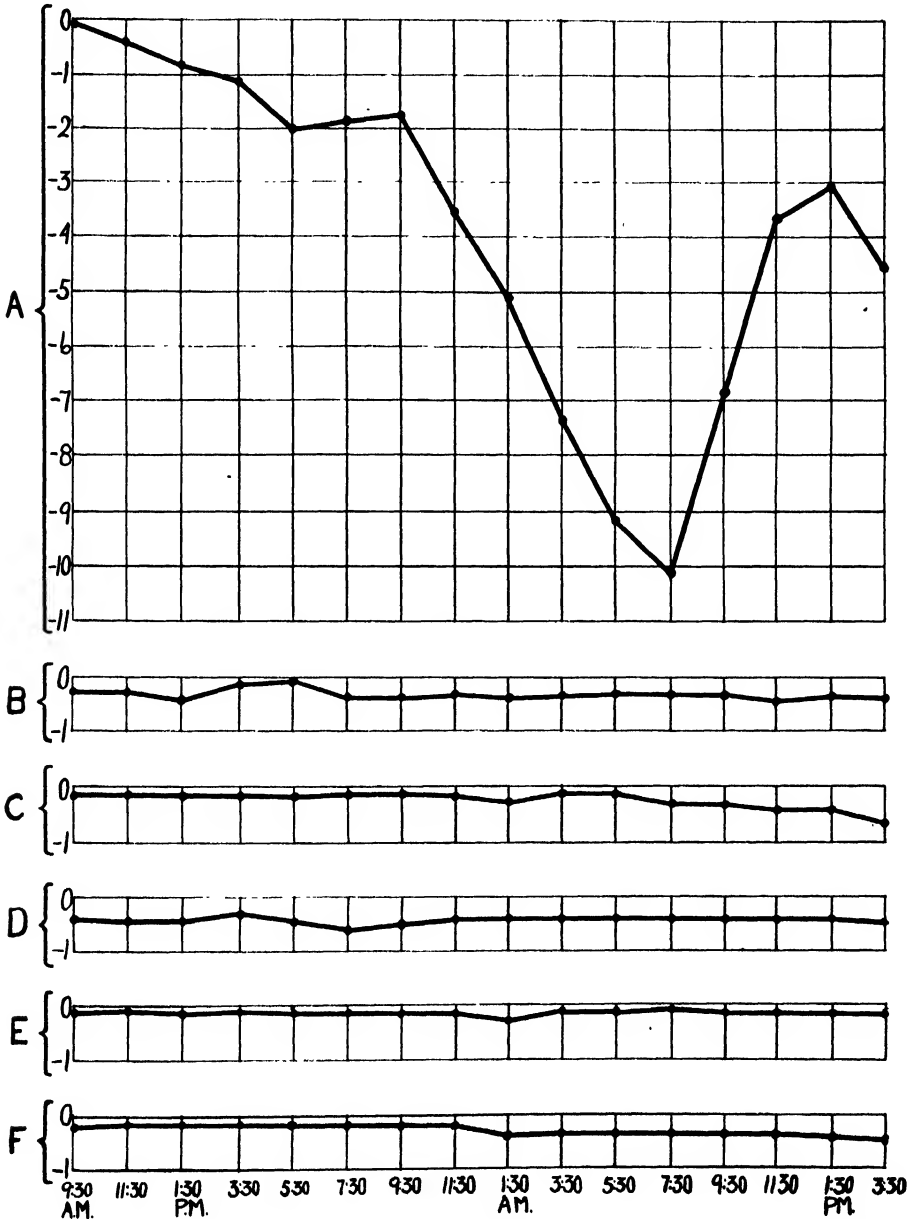


FIG. 4. Diurnal temperatures in hibernacula on February 18-19, 1926, when the hibernacula were covered with 3 inches of snow. Letters A to F same as in figure 2.

TABLE III. *Range of hibernaculum temperatures on February 18-19*

Hibernaculum	Maximum	Minimum	Variation
Air.....	-0.06 C.	-10.3 C.	9.7 C.
Leaves.....	-0.13	-0.49	0.36
Under bark, upper surface, Log I.....	-0.2	-0.66	0.46
Under bark, lower surface, Log I.....	-0.33	-0.6	0.27
Upper surface wood, Log II.....	-0.17	-0.43	0.26
Interior wood, Log II.....	-0.2	-0.49	0.29

variations shown for hibernaculum temperatures doubtless fall within the range of error in the experimental manipulations, as there seems to be no other accountable reason for even these slight fluctuations; they show no relation to the gradually falling and rising atmospheric temperatures, nor with themselves. The important point to be noted here is the relative constancy of temperature within the hibernacula when covered with a blanket of snow, as compared with the widely fluctuating temperature of the air.

Other experiments with little or no snow covering on the ground showed a much greater variation in hibernaculum temperatures. Of course, the more exposed situations (upper surfaces of the two logs) varied much more than the more protected locations (leaves, interior and lower surface of logs).

For purposes of comparison with a warmer season of the year, another 24-hour series of readings was taken on May 21-22, 1926. The results are shown in figure 5. These records were obtained during a sudden fall of atmospheric temperature with frost out of the hibernacula and all of them very moist. Again, the deeper, more protected places in the logs showed a lesser tendency to fluctuate in temperature, and a lag of 5-7 hours in reaching the high and low points in the curves. Temperatures in a layer of moist

TABLE IV. *Range of temperature within hibernacula during the warmer season, May 21-22, 1926*

Hibernaculum	Maximum	Minimum	Variation
Air.....	29.8 C.	7.1 C.	22.7 C.
Under bark, upper surface, Log I.....	28.1	8.3	19.8
Upper surface wood, Log II.....	22.8	10.0	12.8
Leaves.....	18.2	9.9	8.3
Interior wood, Log II.....	17.9	11.4	6.5
Under bark, lower surface, Log I.....	15.7	11.3	4.4

leaves are not as variable as the upper bark and surface wood of the logs, nor as constant as the deeper parts of the logs (Fig. 5 and Table IV). It is probable, however, that when they are dry, they would approach atmospheric temperatures closely.

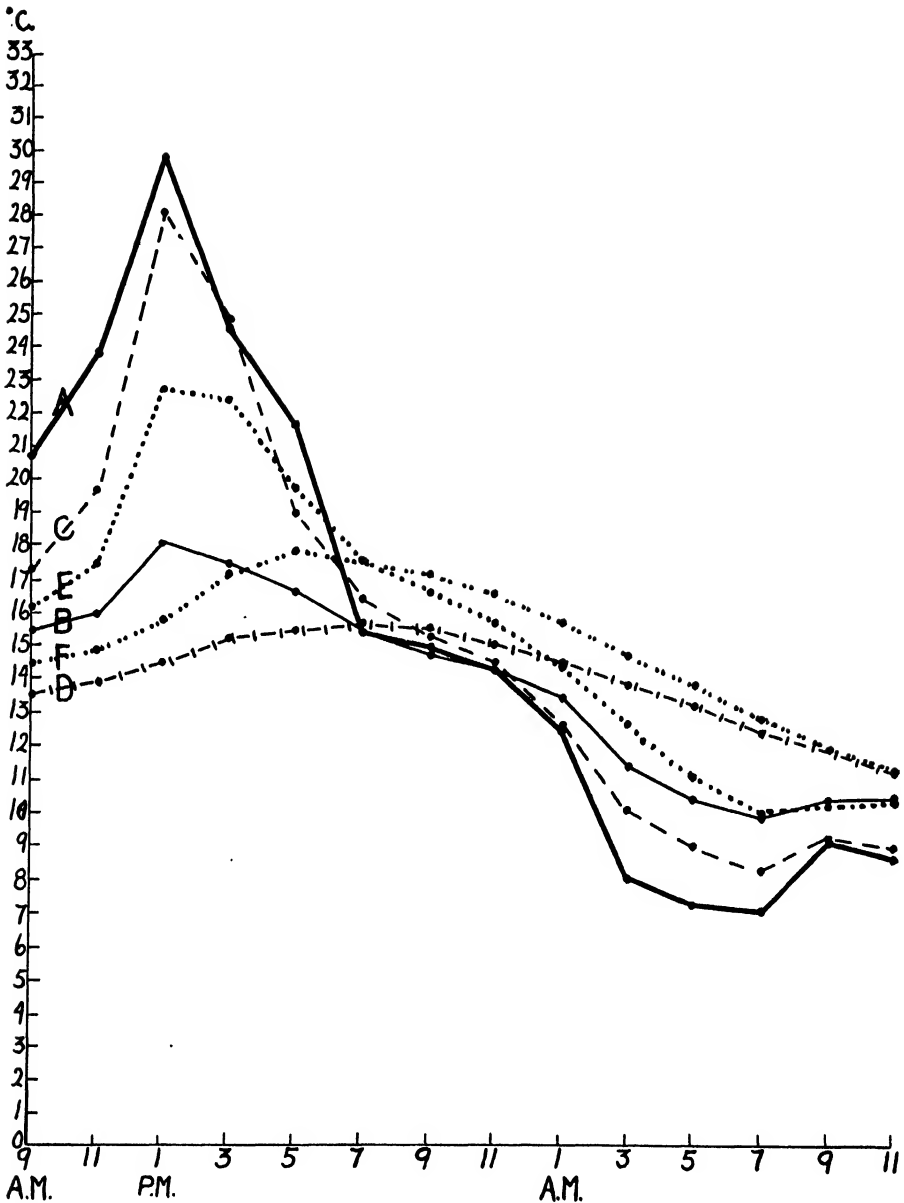


FIG. 5. Diurnal temperatures in hibernacula on May 21-22, 1926. Letters on graphs refer to same locations as in figure 2.

DISCUSSION

It is known that hibernating animals are well protected against the unfavorable temperature conditions of an average winter. The reduction of free water content associated with the lowering of the freezing point, and

the protective super-cooling phenomena of body fluids, are well known (Bachmetjew, Babcock, Payne and others). The retirement to sheltered niches at the approach of winter has always been interpreted as a protective device against the possibility of freezing.

From the above determinations, it is seen that hibernating arthropods obtain a surprising degree of protection in their hibernacula during the winter, even in the more open and exposed conditions of these studies. Indeed, it is doubtful if the temperatures in the more protected hibernacula of the forest ever go below the freezing point of their body fluids. The hibernacula here considered are all characteristic of the forest floor. All benefit by the insulating snow (and sometimes sleet) blanket in regions where snow covers the ground for any considerable part of the winter. In regions further south, the atmospheric temperatures only occasionally approach the danger point. The hibernacula described in this paper are some of the more protected ones. Those arthropods that hibernate in the soil are still more protected; in such a situation, the temperatures below the frost line are always above zero, and even in the frozen surface soil, the temperatures remain very constant at or around the zero point (Holmquist, '28).

A number of arthropod species (Tenebrionidae, Coccinellidae, Muscidae, Thomisidae), however, regularly hibernate in places where they do not benefit by the snow blanket, such as in standing, dead trees and high stumps under very loose, dry bark. These species are undoubtedly not so fortunate. While no determinations were made by the author in these hibernacula, tree temperatures as low as -25.0° F. have been reported (Bourgeau, 1860). Differences as great as 25° C. may exist between temperatures of the north and south sides of trees (Mix, '16), with alternate freezing and thawing on the south side and a much more constant temperature condition on the north side (Harvey, '23). Emerson (1894) found that the temperatures of dead limbs changed more rapidly than those of live ones because of the lower water content. From the investigations of temperatures in living trees, it is quite certain that even more difficult conditions obtain in the over-wintering niches of standing, dead trees, as suggested by Emerson. The species that hibernate in these exposed places must endure widely fluctuating and sub-zero temperatures and must be very resistant to freezing. It is probable that their water content is depressed much more than those which hibernate in more protected places, and therefore that their critical, super-cooling point is greatly lowered. No comparative studies were made on this question.

The most critical part of the hibernating period for arthropods is in late fall and early spring. At these seasons, hibernators are often exposed to sudden, sub-zero weather without the protection of the insulating snow covering and with their water content falling to, or rising from, the low condition of winter. They are therefore much more exposed and much more susceptible to freezing and killing than at any other time of the year. The same exposure to low temperatures may be obtained during a cold, open winter.

A phenomenon that looks like another protection against low temperatures of winter, and one that is rather common among hibernating arthropods is the aggregation of individuals of the same species in the fall for purposes of over-wintering together. Such aggregations may be very small and loose, or very large and densely packed. A series of thermocouple experiments (Holmquist, '28) on temperature conditions in dense clusters of hibernating ants failed to reveal any temperature conservation or heat production comparable to the well known case of the honey bee cluster in winter (Gates, '14, Philips, '14). If such compact aggregations produce no heat, it is not probable that the more common, loose aggregations produce or conserve any.

SUMMARY

1. A series of studies was carried out during the winters of 1924-1925 and 1925-1926 to determine the actual temperatures occurring within certain hibernacula (*i.e.*, among leaves, under bark and in the wood of two logs in middle and late stages of decay respectively). Continuous thermograph records were kept during the first winter, and daily thermocouple readings were taken during the second. The hibernacula were placed in the open near the laboratory buildings.

2. It was found that in late fall and early spring, all hibernaculum temperatures fluctuated with atmospheric temperatures, but less widely. Of the niches examined, the upper surface of the two logs showed the greatest variation, the lower surface and interior wood of the logs showed the least, and the leaves were intermediate.

3. A remarkably constant, zero temperature was maintained in all hibernacula when they were well covered with snow, even though the atmospheric temperatures remained at or below 0° C. for a month at a time. As soon as the snow covering had disappeared, however, hibernaculum temperatures fluctuated, due to the lack of insulation furnished by the snow.

4. The lowest hibernaculum temperature recorded during the two winters of observation was only —8.4° C. This occurred under the bark of the upper surface of an old basswood (*Tilia americana*) log in a late stage of decay during a severely cold wave two days after the first snow fall had occurred, but before the snow had packed enough to establish the stable conditions of winter. The lowest temperature (—5.3° C.) recorded for the leaves during the two winters of observation occurred on the same day. Even these temperatures are considerably above the under-cooling and freezing points of insects.

5. Several sets of thermocouple temperature determinations were made on different days during the winter and spring of 1925-1926 to determine diurnal fluctuations. These showed the same constancy of temperature when the hibernacula were covered with snow, and the same fluctuations when the hibernacula were bare.

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PRELIMINARY REPORT ON THE PHYSICAL ECOLOGY OF CERTAIN PHYLLOPHAGA (SCARABÆIDAE, COLEOPTERA)

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The direct effects of the physical factors such as temperature, moisture, light, barometric pressure, air movement, nutrition, gases of the media, and neutrality of the media on economic pests are little known. This paper comprises a preliminary report based on the studies in 1926 of the first 6 factors named, as they affect the common May beetles in Minnesota.

PREVIOUS ECOLOGICAL WORK

Forbes ('07) takes up the effects of temperature, cold rain, wind, and light on the emergence of the adults. Sanders and Fracker ('16) emphasize the relation of temperature to adult emergence and the activities of the larvae. Davis ('16) deals with life histories, and suggests that latitude has an important influence upon the length of the cycle, but that other factors must be found to explain the variation in local areas.

SEASONAL HISTORY

The May beetles emerge in the spring, feed and mate at night, and oviposit in the soil where they remain hidden during the day. The eggs hatch in 2 to 4 weeks, liberating young grubs that feed upon the roots of vegetation until fall, when they migrate downward to escape the cold. In the spring they work their way back to the surface and continue feeding. The larval stage lasts from 2 to 4 years, at the end of which the grubs form pupal cells in the soil at a depth ranging from a few inches to 2 feet. They pupate and transform the same season in 2 to 4 weeks, but the adults of the species in Minnesota do not emerge until the following spring.

SPECIES STUDIED

The species present at Jordan, Minnesota, in sufficient numbers with which to make careful studies were *Phyllophaga implicita*, *anxia*, *fusca*, and *drakei*. *P. implicita* was the dominant form and the principal one studied. Other species present in fewer numbers were *P. futilis*, *nitida*, and *rugosa*.

¹ These experiments were conducted in 1926 as a part of the white grub project of the Minnesota Agricultural Experiment Station.

EGG STAGE

Eggs were incubated at a series of temperatures ranging from 15° to 30° C., and moisture variations from 9 per cent to supersaturation of the soil (Fig. 1). The eggs were kept in tin salve boxes containing soil. Con-

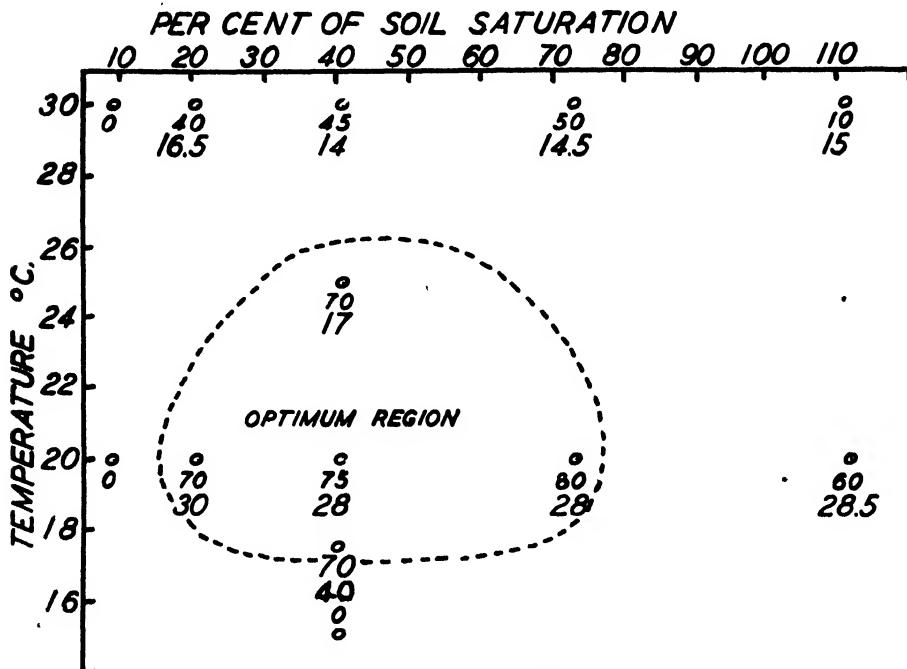


FIG. 1. The effects of temperature and moisture upon the hatching of May beetles. The first figures represent the percentage of hatching, the second the length in days of the incubation period.

stant moisture was maintained by weighing and adding water when necessary. The results in figure 1 at 17.5° were obtained as the average of 20 days' exposure at 15° followed by 20 days at 20°. This shows that very little development took place at 15°, the growth during 20 days being equivalent to that occurring in one week at 20°. Incubation at this latter temperature required 28 days. The time was reduced to 17 days at 25°, and to 14 days at 30°. Uniformly high hatches resulted at 20° and 25°, but the emergence was much reduced at 30°. All of the eggs dried up in a few days in the soils containing 9 per cent of saturation. The supersaturated soils showed a reduction, and although some of the eggs hatched at both 20° and 30°, the grubs were drowned by the excess moisture. Good hatches resulted with moisture conditions between 20 and 73 per cent of soil saturation. Moisture had some effect upon the length of the incubation periods, as a retardation in hatching occurred at the high and low moisture points at both 20° and 30°. The optimum region is indicated in the figure.

LARVAL STAGE

The data secured from studies of the larvae were very incomplete, but are presented with the indications that can be drawn at this time.

Young Grubs. A number of newly hatched larvae were kept at a series of temperatures ranging from 20° to 28° C., and moisture variations from 6 per cent of saturation to supersaturation of the soil (Fig. 2). Six-ounce

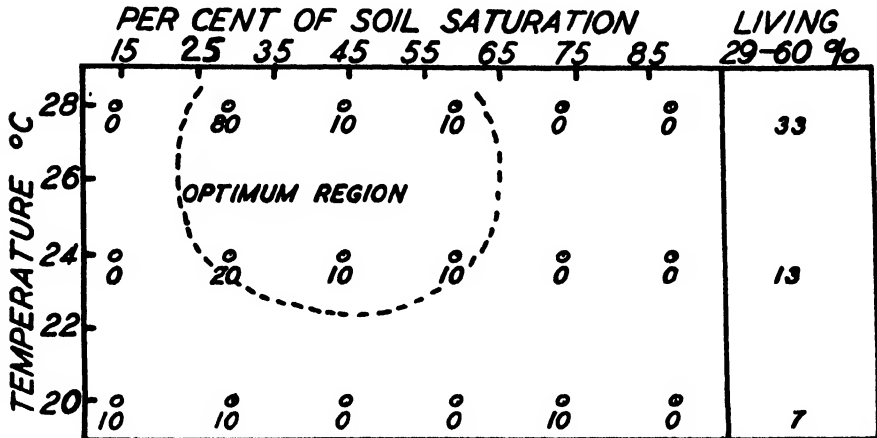


FIG. 2. The percentage of newly hatched May beetle larvae living at the end of two weeks in various temperatures and soil moisture conditions.

salve cans were used as cages. They were examined daily, dead larvae being removed, wheat kernels for food replenished as necessary, and moisture added when below the desired concentration. High mortalities resulted in nearly all conditions, possibly because the eggs had been removed from the surrounding clumps of soil before hatching. The moisture limits were between approximately 25 and 60 per cent of soil saturation except at 20°. The optimum temperature region apparently is well above 20° and appears to be near 28°. A soil moisture content of 29 per cent appears to be far superior to the other percentages of moisture used.

A similar experiment was conducted starting with grubs about a week old (Fig. 3). The optimum region was extended, the older larvae being tolerant to wider ranges of temperature and soil moisture conditions. The higher temperatures still gave better and more uniform results, but the reactions to moisture concentrations were alike within the optimum region. The percentage living was increased at all temperatures, and especially at the lower temperatures.

Old Grubs. Two series of grubs from eggs laid in 1926 were collected during the same season and exposed to different temperatures for extended periods (Table I). One lot of 25 larvae kept at 20° C. for 3 months was feeding less and growing slower than a similar lot, 5 of which transformed,

when held at 25° for the same period. The series at 20° was then raised to 28.5° and 4 larvae immediately pupated, 13 more transforming in the next 2 months, leaving one larva when the experiment was closed. Apparently 20° was too low for metamorphosis to take place. Some of the grubs

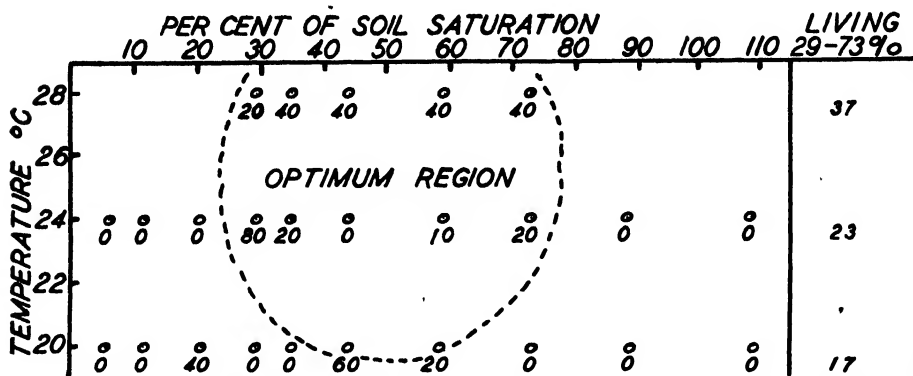


FIG. 3. The percentage of young May beetle larvae living at the end of two weeks at various temperatures and soil moisture conditions.

from this same collection were kept at 28.5°, but the data were not recorded. The death rate was greatly reduced, and the majority transformed much quicker than at 25°, indicating that the higher temperature was more favorable for metamorphosis. The results of Table I were expected and do not

TABLE I. *Effects of temperature on transformation of the larvae of P. implicita*

Soil temp. ° C.	Time in months	No. of grubs	No. transformed	No. dead	No. left
20.0	3	25	0	2	23
28.5	3	23	17	5*	1
25	3	25	5	5	15
27	3	15	11	2	2

* One parasitized.

appear significant until Table II is examined. The grubs used to secure these data were collected in September, 1926, after becoming fully developed. Those kept at 20° did not feed or transform over a period of 5.5 months, at which time the majority of them were very weak but still alive. During the last 2 weeks of the experiment the temperature was raised to about 24°, and 5 pupated, but had not transformed as indicated in the table, when the experiment was closed. In a similar lot held at 20° for 2 months and then raised to 25°, 9 transformed. None of the larvae fed after being collected. This indicated, assuming that *P. implicita* and *rugosa* have the same reaction to temperature, that 20° is too low for pupation, yet too high for overwintering. The necessity for temperatures as high as 24° to 28° for pupa-

tion is an important factor in extending the life cycle under natural conditions. The adults reared from the grubs used in securing the data in Table I were *P. implicita*, and in Table II were *P. rugosa*.

TABLE II. *Effects of temperature on transformations of the larvae of P. rugosa*

Soil temp. ° C.	Time in months	No. of grubs	No. transformed	No. dead	No. left
20	5.5	25	0	2	23
24	0.5	23	5	0	18
20	2.0	25	0	0	25
25	4.0	25	9	12	4

Feeding. Feeding practically stopped when the temperature dropped down to 15° to 16° C. Other activities were reduced, but burrowing through the soil continued below 15°. The upward migration of the larvae in the spring begins before the temperature of the surrounding soil reaches 15°. Sanders and Fracker ('16) found the effective soil temperature to be between 15.5° and 18.3°.

Over-wintering. Field experiments were conducted in the winter of 1925-1926 to test the ability of the last instar larvae to withstand low temperature (Table XII). All that were above the frost line were killed. Those below the frost line, but at 0° C., lived. Field digging in the spring of 1926 where the grubs were free in the soil corroborated this, as all (16) last instar larvae found above the frost line were dead. Two individuals of younger stages were found alive in frozen soil that had experienced temperatures at least as low as -4°. Perkins (1892) reported finding grubs feeding under a foot of snow, and also says that some were active in frozen soil. Later, in box experiments, he found that temperatures slightly below freezing killed all of the larvae. Davis ('13) states that grubs of *P. tristis* were able to live over winter in frozen soil.

Artificial Freezing. The undercooling and freezing points of grubs past the feeding stage and approaching pupation, compared with larvae still feeding, are given in Table III. All temperatures were taken internally with

TABLE III. *Body temperatures, undercooling points, and freezing points of white grubs*

No. of grubs	Soil temp. ° C.	Body temp. ° C.	Undercooling points ° C.	Observed freezing points ° C.	True freezing points ° C.
Not feeding					
9	21.3	21.4	-3.4	-1.6	-1.5
5	28.5	26.9	-4.8	-1.7	-1.6
Feeding					
9	8.5	10.5	-4.2	-1.5	-1.4
5	28.5	26.6	-4.5	-1.2	-1.1

the aid of a thermocouple. The penetration of the body wall by the thermocouple junction may have affected the body temperature of the grubs. The observed freezing points were corrected by the formula $\Delta = \Delta' - 0.0125u\Delta'$, where Δ is the true freezing point, Δ' the observed freezing point, and u the undercooling point (Harris and Gortner, '14). The undercooling and freezing points as found cannot be considered a measure of the ability of the grubs to withstand low temperatures, although freezing, as the condition is recognized, produces death. However, the data in Tables III and XII are in very close agreement. The ability to maintain a body temperature above or below the surrounding environment is demonstrated. The soil at 8.5° had been constant for about 12 hours and had varied between 4° and 15° for about a month. The other temperatures had remained constant for about a month. At 8.5° the body temperature is maintained 2° higher, at 21° it is in equilibrium with the soil, and at 28.5° it is 2° lower than the soil.

Moisture Content. The moisture contents of the larvae are shown in Table IV. The results are almost identical with the moisture contents found

TABLE IV. *Moisture content of white grubs*

Previous temp. ° C.	No. of grubs	Total water, per cent	Free water, per cent of total	Percentage of bound water
20°—3 mon. . . .	5	77.7	91.4	8.6
0.5°—6 wks. . . .	3	79.4	88.3	11.7
0.5°—7 wks. . . .	4	77.7	86.9	13.1

in the adults (Table XVII). Since the free water freezes, while bound water does not, at temperatures above — 20° C., the amounts of each present are very important to the organism (Robinson, '27). The free water comprised 87 to 91 per cent of the total water content of 78 to 79 per cent. Therefore it is to be expected that the larvae would not have great ability to withstand low temperatures. Furthermore, the results indicate that larvae kept at 0.5° for 7 weeks had very little physiological ability to acquire winter hardness.

Periodicity. The question has been asked whether white grubs show any periodicity, or whether it is merely a reaction to climatic conditions that controls the length of the life cycle. Larvae from eggs collected in the spring of 1926 and maintained at temperatures between 20° and 28° C. transformed into adults without any definite rest periods except at times of molting (Table V). A total of 58 individuals were reared, all *P. implicita*. The average

TABLE V. *Development of larvae of P. implicita when kept under continuous artificial summer temperatures, between 20° and 28° C.*

No. of larvae transformed	No. of days to transform
9.	212-219
4.	220-227
7.	233-239
15.	240-248
14.	250-258
9.	260-269

period from hatching to the adult stage was 8.08 months. Ninety-eight grubs, newly hatched, collected at the same time transformed into adults during the experiment. The shortest developmental period was 7.07 months. All adults reared were *P. implicita*, but, because of the short duration of the experiments, other species with a slightly longer cycle may not have had an opportunity to complete the larval development. These results indicate that the length of the life cycle of *Phyllophaga* is dependent upon ecological factors.

ADULT STAGE

Minimum Limiting Temperature. The minimum limiting temperature depends upon the previous environment the insects have lived in, the time and rate of change of temperature, and the reactions of the organisms selected as criteria. In the following experiments the beetles were placed at 0° C. until inactive, then the temperature was raised at the rate of 2° in 5 minutes until the insects began walking. The points selected for minimum temperature effects were "first move," "one feet," and "walking." When the May beetles became inactive at 0° they fell on their backs or sides, since the surface was smooth. They are rather active when able to remain on their feet on a smooth surface of moderately fine soil. From this point the activity increased rapidly as the temperature was raised. They usually began walking immediately after regaining their feet. The results for 6 species are given in figure 4. The influence of previous history is well illustrated in comparing the reactions of *P. implicita* that had been feeding in the field with those that had been kept in storage at 0°, the latter responding at temperatures several degrees higher than the former. It will be seen that the first reaction at the lower temperature was very similar for the 6 species, a spread of only 2.6° existing between them. When the temperature became sufficient for them to regain their feet a spread of 11° existed. It is interesting that the temperature at which the various species from the field regained their feet corresponds to the order of their appearance in the spring. *P. fusca* appeared April 29, about one week ahead of *P. anxia*, then a few days later *P. implicita* and *drakei* emerged. *P. rugosa* was first found on May 31 and *P. nitida* on June 6, neither being found in sufficient numbers to be compared accurately with the other species.

Maximum Limiting Temperature. The reactions to high temperature were secured for 3 species, and are shown in figure 4. The first evidence of paralysis at high temperature occurred at almost the same point, there being only 0.6° C. spread for the 3. When the inactive state was reached, only 0.2° difference remained. It is very interesting that a group of insects so nearly similar in habits, and with the limiting temperatures so much alike, should show such a wide difference in their reactions to temperature in the central portion of the active zone.

Emergence. Emergence for the first time depends upon the cumulative

effects of heat. Criddle ('18) makes the statement that May beetles migrate upward in the spring and wait for the first really warm evenings to emerge. Beetles dug up in the field on April 16 just above the frost line, so that very little effect of spring heat could have taken place, and kept under controlled

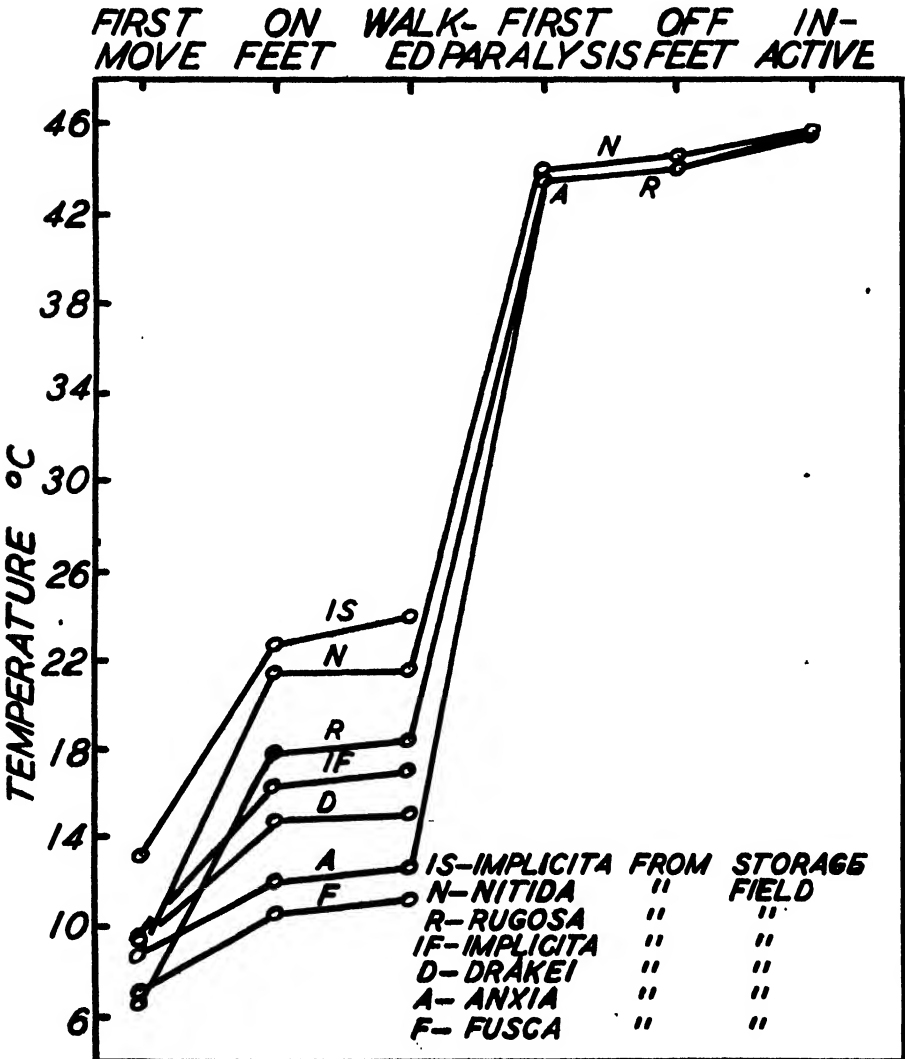


FIG. 4. The minimum and maximum limiting temperatures of *Phyllophaga*.

conditions in clay pots containing soil, demonstrated the cumulative effects of temperature upon first emergence (Table VI). *P. implicita*, maintained at 20°, 25°, and 30° C., did not emerge the first evening at the given temperatures but required an average of 8.2, 4.2, and 4.5 days respectively. The

TABLE VI. *Emergence of P. implicita and P. futilis under constant temperatures*

Temperature ° C.	No. emerged	No. not emerged	Hours to emerge	Equivalent in days
<i>P. implicita</i>				
11	2	15	684	28.50
17	3	12	416	17.33
20	19	0	197	8.21
25	19	0	101	4.21
30	18	0	109	4.54
<i>P. futilis</i>				
14	10	3	547	22.79
20	12	0	169	7.04

shortest period for emergence occurred at 25°, while a slight retardation is shown at 30°. Emergence was greatly reduced below 20°, and was at a minimum at 14°. Since the 30° temperature did not shorten the time necessary for emergence, it indicates that the optimum is much nearer 25° than 30°. *P. futilis* emerged in 23 days at 14°, while only 7 days were required at 20°, showing that a smaller amount of warmth is required for the emergence of this species unless previous cumulative effect had taken place before collection, as these were collected later than *P. implicita*.

The effects of varying temperature upon emergence of *P. implicita* are shown in Table VII. Apparently very little cumulative effect took place at

TABLE VII. *Emergence of P. implicita under varying temperatures*

Temperature ° C.	No. emerged	No. not emerged	Hours to emerge	Equivalent in days
14 (16 hrs.), 20 (8 hrs.)	13	2	305-162	12.71-6.75
14 " 25 "	14	4	279-140	11.62-5.83
14 " 30 "	17	1	240-124	10.00-5.17
20 " 30 "	17	1	86-38	3.58-1.58
20 (20 hrs.), 30 (4 hrs.)	9	0	125-23	5.21-0.96

14°, as the time at the higher temperature is about equal to the time necessary for emergence at the respective temperatures in Table VI. Probable errors were sufficient to explain the discrepancies between the 2 tables.

The upward migration of the adults of *P. implicita* had not started on April 16, 1926, at Jordan, Minnesota. Most of the beetles were still in the pupal cells from 5 to 15 inches in depth, indicating no movement since transforming in the previous fall. The temperatures at the surface, 6, and 12 inches were 12°, 5.25°, and 1.5° C., respectively. The ground was frozen to 15 inches below the surface.

TABLE VIII. *Soil and air temperatures of a corn field free of weeds and grass at Jordan, Minnesota, at the time of emergence of Phyllophaga*

Date	Air temp. ° C.		Soil temperature ° C.						
	4.5'	2"	0"	1"	2"	3"	4"	5"	6"
5-5-26	23.0	26.00	19.25						16.25
6	20.5	19.00	21.25						18.75
7	20.0	19.00	20.75						19.75
8	15.9								
9	11.1								
10	9.1								
11	11.5								
12	14.5	15.50	17.75	15.00		16.00			18.30
13	5.5								
14	8.5								
15	18.5	18.50	18.50	20.00	20.00	20.00	20.00		
16	16.6	17.75	18.00	17.30	16.75	17.00			
17	15.0	14.50	15.00	17.50	17.50	19.25	19.25	19.00	18.50
18	10.5								
19	11.8								
20	14.0	15.50	15.25	15.50	16.50	16.50	16.50	16.50	
21	6.0	9.00	8.00	9.00	10.00	10.50	11.00	11.00	12.00
22	11.0	11.25	11.50	12.25	14.00	15.60	17.00	17.00	17.25
23	21.0	18.50	22.50	22.50	22.75	23.00	22.75	22.00	21.25
24	23.5	21.50	22.00	22.00	22.00	22.30	21.75	21.50	20.00
25	25.7	24.00	23.00	23.25	23.50	23.25	22.75	22.00	21.00
26	17.8	18.00	20.00	21.25	22.25	23.00	22.80	22.00	21.50
27	16.2								
28	20.5	20.00	20.00	21.00	21.00	21.50	21.25	21.25	20.75
29	17.8	19.50	20.00	21.00	21.75	22.25	22.00	21.50	20.00
30	23.5	24.30	23.00	25.30	26.00	26.00	26.00	25.30	24.30
31	12.5	14.80	13.30	14.50	15.30	17.00	18.00	18.30	18.50
6-1-26	11.5								
2	8.5								
3	10.0	14.80	18.50	18.00	19.00	19.30	18.80	18.00	17.50
4	11.2	12.00	13.00	16.30	17.30	19.00	19.00	19.00	19.00
5	22.2	25.50	24.00	24.00	22.80	22.80	21.60	20.50	19.20
6	18.5	19.00	18.50	19.20	19.50	19.50	20.00	20.00	20.00
7	19.0	18.00	18.00	18.50	19.50	19.50	19.50	19.50	19.20
8	16.1	13.00	15.00	19.00	20.00	20.50	20.00	20.00	19.50
9	19.5	19.50	20.00	22.30	23.90	24.10	23.50	23.50	22.30
10	20.5	22.50	21.50	21.80	22.50	22.50	21.80	20.80	20.50
11		23.50	23.90	25.30	26.20	26.50	26.20	25.00	23.90

Flights of *P. implicita* were not general until May 12, although soil temperatures were above 14° C. in the upper 6 inches as early as May 5 (Table VIII). The males tend to come out slightly earlier than the females, as the males were predominant in the early collections. Furthermore, in a field emergence experiment, 29 males came out while 22 females were emerging (Table IX). The beetles were dug up and caged in the same soil in the field, the only limitations being to prevent lateral and depth migrations. Eight females and one male, 11 per cent, remained on May 22. The slow emergence may be explained by individual differences, or more probably by the cumulative effects of the previous season. Transformations into adults in July would permit more time for the effects of heat accumulation than August

transformations, and, consequently, the former might be expected to emerge earlier in the spring. May was a warm month and should have facilitated emergence. The temperature dropped below freezing on May 3, but warm weather followed, so that the mean temperature for the month was 2.7° C.

TABLE IX. *Emergence of P. implicita under natural conditions*

	No. of beetles	Number emerged on May										No. left
		6	7	8	10	15	16	17	20	21	22	
Males	30	1	0	1	1	14	10	0	2	0	0	1
Females	30	0	4	1	3	1	9	1	3	0	0	8

(4.8° F.) above normal at Minneapolis, 32 miles from Jordan. June, with the exception of 2 brief periods, was cold throughout.

Daily emergence occurs regularly whenever the conditions are suitable. Sanders and Fracker ('16) found that emergence was greatly reduced for a number of species, including those mentioned in this paper, at 18.9° C. and ceased at 16.8°. They gave no information regarding their methods of taking the temperatures. Forbes ('07) reports that no beetles were ever taken when the minimum temperature for the day was below 11° C., but does not give the lowest temperature at which adults were taken. The minimum referred to by Forbes occurred after midnight in every case, so did not affect the emergence. The minimum temperature for emergence of *P. implicita*, *anxia*, *fusca*, and *drakei* appears to be about 14° at the soil surface, and emergence increases rapidly for the next few degrees of rise in temperature (Fig. 5). This agrees with laboratory experiments (Table VI). The numbers of each species collected are given in Table XVIII. Air temperatures were taken at 2 inches and 4.5 feet above the soil surface; soil temperatures at intervals of one inch from the surface to a depth of 6 inches. The surface temperature shows a close relationship with emergence and seems to determine whether beetles will emerge or not. Temperatures were taken in woods, grassland, and a corn field that was free of weeds and should be considered as fallow land until the corn came up in the latter part of May. Records for the surface temperature of the corn field at the time of emergence are given in Table VIII. In figure 5, the surface temperatures of the 3 areas are plotted, showing that one area might have a surface temperature below the emergence point, while the others were above. Controlled experiments bear out this conclusion, as only 2 adults of *P. implicita* emerged from the soil after 28 days at 14° (Table VI). *P. futilis* will emerge at a slightly lower temperature which has not been determined at present. This is readily shown in Table VI as only 16 per cent of *P. implicita* emerged below 20°, while 77 per cent of *P. futilis* emerged below 20°. It is not inability to fly at low temperatures that prevents emergence, since the May beetles are

capable of making strong flights in the morning with temperatures as low as 5° . When once emerged they do not return to the soil because of low temperature. A long period of cold weather might make adults emerge because of starvation, and feed upon vegetation in the field without flying, but

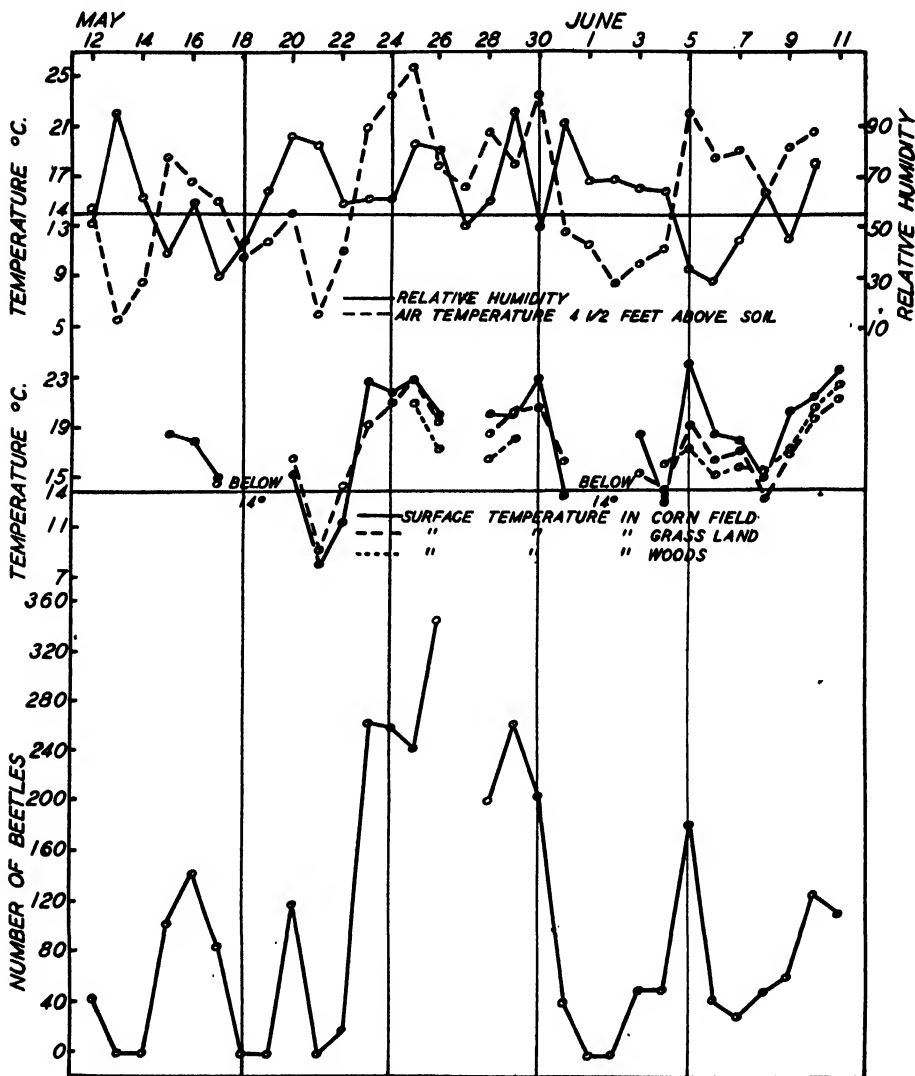


FIG. 5. The number of May beetles collected from twenty-five food plants on successive evenings, with the surface and air temperatures and relative humidity at the time of emergence. For species collected see Table XVIII.

no evidence in support of this view was observed. The largest numbers were collected from plants from May 23 to May 30 when the surface temperatures were 20° or higher (Table VIII and Fig. 5). It is evident that whenever

the soil surface exceeded 20° beetles were numerous on food plants. A study of the last column in Table VI shows a reduction in time for emergence of *P. implicita* as the temperature increased from 14° to 25°, with a retardation taking place at 30°. *P. futilis* responded more quickly to 20°, but these specimens were not collected early enough to avoid the spring increase in soil temperature. Sanders and Fracker ('16) found that the maximum flight was not always at the highest temperature.

Moisture in the form of relative humidity, precipitation, soil moisture, or evaporation had very little effect upon emergence. Precipitation will, if sufficient to produce mud, prevent digging out, but May beetles will emerge during a rain if the temperature is high enough. Forbes ('07) states that cold, heavy rains prevented, but that moderate rains did not affect emergence, and that feeding continues if a storm comes up. Soil moisture reduces the temperature and thus indirectly operates upon emergence. The rate of evaporation from a Livingston atmometer when the beetles begin flying is so slight that it may be disregarded in so far as it affects emergence; but during the day the soil is dried out. Relative humidity apparently has no direct influence, as the beetles emerged under wide variations in humidity (Fig. 5).

Oviposition. The eggs of *P. implicita*, *fusca*, *anxia*, and *drakei* were found in the field from May 20 to 24, 3 weeks after the first emergence of the males and 10 to 14 days after most of the females emerged. Eggs,

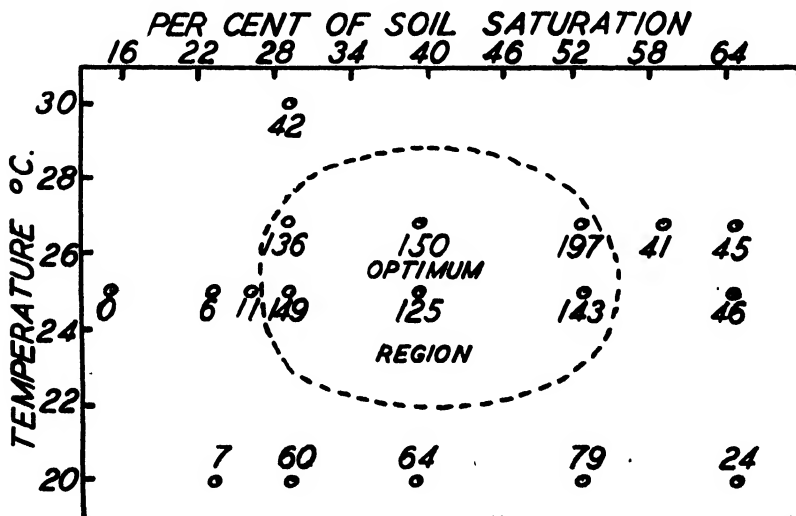


FIG. 6. The number of eggs laid by *Phyllophaga implicita* at various temperatures and soil moisture conditions.

apparently mature, were found in females 5 to 10 days after emergence. Adults of *P. implicita* that emerged in the laboratory were maintained at constant and varying temperatures in glass jars containing soil with a moisture

content ranging from 15 to 65 per cent of saturation (Fig. 6). The moisture content was maintained by weighing and adding water when necessary. The soil was mixed thoroughly whenever water was added. The data in figure 6 were taken from 3 series held at constant temperatures of 20°, 25°, and 30° C., and one held at a varying temperature, 25° to 30° with an average of 26.7°. The cages at 20° and 30° are clearly beyond the range of the optimum region, but more eggs were laid at 20° than at the corresponding point at 30°, indicating that the optimum would extend further below 25° than above that temperature.

The effects of moisture are evident, as oviposition is sharply limited at the high and low percentages of saturation. At 25° C., with a saturation of 26.5 per cent, only 11 eggs were laid by 5 females, but at 29.4 per cent of saturation, the same number of females laid 149 eggs. The high moisture limit is similar, as 197 eggs were laid at 53 per cent of saturation and only 41 at 59 per cent at 26.7°. At 20° and 25° the same sharp limit is shown. In natural conditions it was found that eggs and newly hatched larvae were much more plentiful in moist than in dry fields (Sweetman, '27). This is further illustrated, in Table X, with a study of *P. implicita* and *anxia* which

TABLE X. *Effects of soil moisture on oviposition of P. implicita and P. anxia*

Species	Temp. ° C.	Days of experiment	Percentage of soil saturation	No. of eggs
<i>anxia</i>	25	15	26.5	2
".....	25	15	44.1	16
".....	25	15	88.2	0
<i>implicita</i>	25	15	26.5	17
".....	25	15	44.1	69
".....	25	15	88.2	15

demonstrated the effects of soil moisture on oviposition. The 5 females for each cage in this experiment were collected in the field after the peak of the egg laying season was over. *P. anxia* did not lay any eggs in the soil with the high moisture content, and only 2 eggs in the soil with a moisture content below 29 per cent of saturation, while 16 eggs were laid in the soil with approximately 44 per cent of moisture. *P. implicita* showed the same reaction, with more than 4 times as many eggs in the 44 per cent soil as were laid in the soils with 26 and 88 per cent of saturation. When the soil moisture drops below 29 per cent of saturation many of the females die in a few days, while at the high limit they are capable of toleration for extended periods but do not reproduce. In the field, the beetles probable do not remain in unfavorably dry soils for more than a day or two in succession. It will be recalled that the soil moisture content necessary for the incubation of the eggs (Fig. 1) agrees rather closely with the moisture requirements for longevity and egg production.

Table XI contains data showing the effects of constant temperature on oviposition of *P. futilis*. The superiority of 20° C. over 25° for egg production is clearly seen. In comparing this with the egg laying of *P. implicita* (Fig. 6) it is evident that the optimum regions are different for the 2 species.

TABLE XI. *Effects of constant temperature on the oviposition of P. futilis*

Temperature ° C.	No. of eggs
20.....	135
25.....	49

Over-wintering. Apparently May beetles do not harden to withstand winter conditions. The adults of *P. implicita* live over winter in the pupal cells unless disturbed. Field experiments were conducted in the winter of 1925-1926 to determine the minimum temperature which the adults of *P. implicita* could endure. The beetles were buried in cages at depths of 0.5, 1, 1.5, 2, 3, 4, 5, and 6 feet (Table XII). The temperatures were determined

TABLE XII. *Ability of May beetles to withstand low temperatures in their natural environment*

Feet in soil	Adults		Grubs		Lowest temperature ° C.
	Alive	Dead	Alive	Dead	
0.5	0	9	0	2	-8.00
1.0	1	9	0	2	-6.75
1.5	3	7	0	2	-5.25
2.0	7	3	0	2	-3.75
3.0	10	0	0	2	-1.75
4.0	10	0	1	1	0.00
5.0	10	0	2	0	0.00
6.0	6	4	2	0	0.00

by the use of thermocouples buried in the fall and read on alternate days. They stood at the low point recorded for about a week. One beetle withstood a temperature of -6.75° C. for one week, while 9 succumbed to this temperature. Three lived and 7 were killed at a temperature of -5.25°, indicating that soil temperatures below -5° are disastrous to the species.

The freezing and undercooling points for *P. implicita* were taken with thermocouples placed under the elytra of the beetles (Table XIII). Insects

TABLE XIII. *Freezing and undercooling points of P. implicita under artificial conditions*

Previous history	No. of beetles	Undercooling points ° C.	Observed freezing points ° C.	True freezing points ° C.
0° C.—3 wks.....	5	- 5.35	-2.87	-2.68
Oct. 30—field.....	3	-10.58	-7.58	-6.58
7° C.—3 wks.....	2	- 3.62	-1.45	-1.38
22° C.—3 wks.....	5	- 7.90	-3.90	-3.52
33° C.—3 wks.....	3	- 5.40	-2.12	-1.98
8 days old.....	1	-10.40	-4.00	-3.48
Average.....	19	- 6.94	-4.01	-3.27

of various ages, one week to one year, were used. These were taken from wide extremes of temperature, 0° to 33° C., at different times of the year, to test the effects of previous conditions upon freezing and undercooling. It is interesting that temperature, age, and feeding or not feeding did not make any appreciable change in the results. The beetles brought in from the field on October 30 had a lower average freezing point than the others, but this may or may not be significant as it does not agree with the evidence in Table XII, where 70 per cent were killed at -5.25° . The first freezing, at the time of the rebound, did not kill the adults if they were removed immediately from the cold chamber following the determinations; but if freezing was permitted to continue for a few minutes death always resulted. Payne ('26) found that previous temperatures had a very important influence upon the freezing of oak borers. The average freezing point for *P. implicita* was -3.27° .

TABLE XIV. *Freezing points of May beetles obtained by artificial freezing*

Previous history	No. of beetles, <i>P. implicita</i>	Freezing points $^{\circ}$ C.
0° C.—winter.....	4	-3.75
7° C.—3 weeks.....	1	-0.90
12° C.—3 weeks.....	3	-2.88
22° C.—3 weeks.....	11	-4.75
Average		-3.99
<i>P. anxia</i>		
Feeding.....	4	-4.11

Table XIV gives the freezing points of *P. anxia* and *implicita* when the undercooling points were not taken. Again, for 22 individuals of *P. implicita* the average observed point was -3.99° , which agrees with the data in Table XIII. Four specimens of *P. anxia* had an average observed freezing point of -4.11° , which is very close to that found for *P. implicita*.

The cooling of the soil in the field is a gradual process, and time is an important element in the freezing phenomenon. Records of time and freezing were kept for 2 sets of beetles exposed to low temperatures (Table XV).

TABLE XV. *Effects of low temperature and time upon the freezing of P. implicita*

No. of beetles	Temperature $^{\circ}$ C.	No. of hours	No. frozen	Result of freezing
9	-3	4	0	
9	-5	28	1	dead
8	-5	42	1	"
7	-7	6	2	"
5	-7	9	1	"
4	-7	24	2	"
2	-11	11	2	"
12	-1	53	0	alive
12	-7	1	2	"
10	-10	14	8	"
2	-11	11	1	"

In the first series, one was frozen at the end of 28 hours at $-5^{\circ}\text{C}.$, another in 42 hours. At -7° two were frozen in 6 hours, one in 9, and 2 after 24 hours, leaving 2 that withstood -11° for 11 hours. In the second series one was alive and normal after 11 hours at -11° .

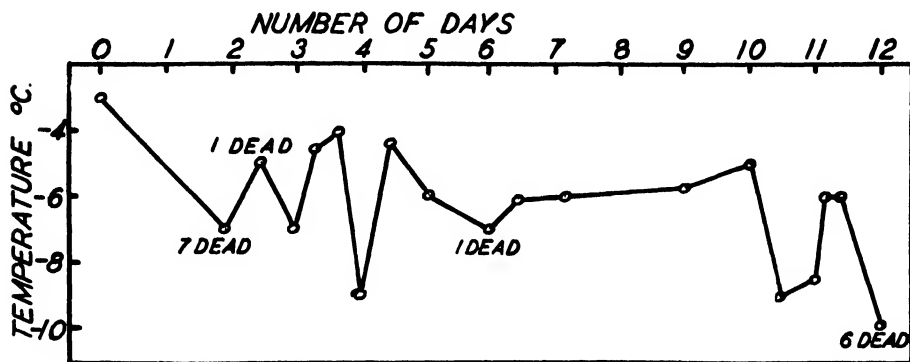


FIG. 7. The ability of May beetles to maintain a body temperature above that of an environment below freezing.

The results of another series is plotted in figure 7. The influence of the length of the exposure is shown to be very important, and may be more so than lower temperatures for shorter periods of time.

It is not generally recognized that insects are capable of maintaining an internal temperature several degrees above the surrounding environment when exposed to low temperatures. The 6 beetles shown in figure 7 that were still living on the eleventh day when the temperature was $-6^{\circ}\text{C}.$ or lower, for the previous 24 hours had an average internal temperature of 3.1° (Table XVI). This is 9° above the temperature of the surrounding soil. The day preceding the determinations the temperature was -9° , but the following day freezing and death of the insects resulted at -10° .

TABLE XVI. *Body temperatures of beetles when exposed to temperatures below freezing*

Beetle number	Internal temperature ° C.
1.....	5.2
2.....	1.1
3.....	2.4
4.....	1.8
5.....	2.6
6.....	5.5
Average.....	3.1

Payne ('26) found the moisture content to be important in the freezing of oak borers, and Robinson ('27) has found the same to be true of the rice and granary weevils. Moisture determinations made by the electrical method described by Robinson ('26) of newly emerged and old specimens, some of which had been feeding, demonstrated that the free moisture content of the

species was nearly constant under wide extremes of conditions (Table XVII). If the free moisture content of May beetles is an index of their ability to withstand low temperatures, the similarity of the insects under different conditions would indicate that the freezing point does not change throughout the year. This agrees with the results in Table XIV.

TABLE XVII. *Moisture content of May beetles*

Previous history	Species	No. of beetles	Percentage of free water
Winter ° C.	<i>implicita</i>	23	77
Feeding.	"	16	77
Two mon. old—no food.	"	1	78
One " " " "	<i>anxia</i>	5	74
One " " " "	<i>rugosa</i>	1	77

Light. Forbes ('07), with the aid of several assistants, found that emergence was nearly simultaneous in the evening over an extended area. A few species are day fliers with habits somewhat different from the night fliers (Hayes, '19). Studies in Minnesota show that when the light diminishes to a definite intensity in the evening the beetles emerge, provided other conditions are suitable. The reaction of the beetles is not nearly so definite in the morning. Some return before break of day and other continue feeding until almost sunrise, although there is a major flight when many beetles will be seen returning to the field in a few minutes. Forbes ('07) makes the statement that the morning flight lasts only a few minutes. The appearance of the adults in dark woods was noticeably ahead of those in the open fields. In dark chambers with constant temperature the majority came out in the evening, indicating a daily periodicity regardless of light intensity. When once emerged, strong artificial light will make some return to the soil.

Barometric Pressure. Air pressure did not have any detectable influence on the beetles. Emergence appeared to be independent of a rising or falling barometer. Rhumbler ('25) suggests the possibility of air pressure changes starting the flights of *Melolontha*, a closely related genus in Europe.

Movements of the Air. Wind is an important factor at times in the life of May beetles. Evening winds do not have very much influence unless strong. In these cases emergence is not affected, but the direction of flight must be with the wind, and feeding must be low and on the protected sides of plants, since the insects cannot cling to the leaves to feed where exposed. A statement by Forbes ('07) credits high wind with preventing emergence. Collections are much harder to make during strong winds, but persistence will reveal many specimens. On the other hand, feeding is on the uppermost branches of the food plants on calm evenings.

Food Relations. A study of abundance of May beetles is very difficult to make under field conditions if tall trees are present. Wind has an important influence upon the numbers collected. The species shown in Table

XVIII were collected by nightly visits to the same plants, 25 in number, between 9 and 12 o'clock at night. Because of the influence of large trees, a comparison of abundance between species cannot be made. Only a comparison of numbers on successive evenings for each species is possible. Collections by light traps were too inaccurate to be used for quantitative purposes.

TABLE XVIII. *Number of May beetles collected from 25 food plants on successive evenings. For temperature conditions see figure 5*

Date	Number of beetles collected				Total number
	<i>implicata</i>	<i>anxia</i>	<i>fusca</i>	<i>drakei</i>	
5-12-26	3	37	1	3	44
13	0	0	0	0	0
14	0	0	0	0	0
15	20	83	2	1	106
16	41	98	2	1	142
17	5	64	10	7	86
18	0	0	0	0	0
19	0	0	0	0	0
20	11	81	0	26	118
21	0	0	0	0	0
22	1	9	0	7	17
23	57	181	2	25	265
24	90	140	4	25	259
25	90	114	10	27	241
26	197	117	24	12	350
28	79	90	15	18	202
29	58	172	18	17	265
30	73	90	24	21	208
31	1	39	3	0	43
6-1-26	0	0	0	0	0
2	0	0	0	0	0
3	3	37	3	9	52
4	10	29	6	7	52
5	45	111	18	10	184
6	1	38	5	1	45
7	8	17	4	5	34
8	7	34	5	4	50
9	11	41	4	7	63
10	50	71	3	5	129
11	59	43	3	10	115
Totals	920	1736	166	248	3070

The food plants of a particular species of *Phyllophaga* vary in different localities, probably according to availability. Table XIX gives the plants on which beetles were found feeding. *P. implicata*, *fusca*, and *drakei* fed almost entirely upon woody plants, while *P. anxia* proved to be a much more general feeder, eating a number of herbaceous plants. Dawson ('22) and Hayes ('20, '25) record a number of weeds and grasses that May beetles feed upon. This varied food habit may be an important method of maintaining infestations more than one-eighth of a mile from trees. The relation of food plants to places of oviposition has been taken up in a previous paper (Sweetman, '27).

The odor of food plants may have some effect upon the direction of flight. The writer has found that *P. implicita* will come to a willow twig if carried in the field, especially when the leaves are bruised. Also, there is some evi-

TABLE XIX. *Food plants of May beetles in Minnesota*

anxia	implicita	fusca	drakei
Preferred plants			
willow ash elm lilac	willow poplar	ash oak	ash oak wild rose
Other food plants			
boxelder plum, blossoms and leaves apple, blossoms and leaves birch poplar currant wild rose chokecherry hazel nut spirea gooseberry raspberry dock nettle artichoke giant ragweed strawberry goldenrod peony	elm plum apple oak ash boxelder birch wild rose lilac hazel nut currant dock goldenrod nettle	elm boxelder plum willow poplar lilac wild rose hazel nut raspberry	elm willow plum apple poplar birch lilac currant raspberry

dence that they will go toward trees regardless of air currents, when these are not too swift, and they often came to the writer in open fields. These incidents may indicate that the beetles fly towards any outstanding object. Rhumbler ('25) states that the *Melolontha*, a closely related genus in Europe, direct their flight through the smell and sight organs.

SUMMARY

Egg Stage. The optimum temperature for incubation of the eggs of *P. implicita* and *anxia* was near 25° C. Twenty to 73 per cent of saturation of the soil gave satisfactory moisture conditions.

Larval Stage. The optimum temperature for development of the young larvae of *P. implicita* and *anxia* was near 28° C. Twenty-five to 75 per cent of saturation of the soil gave satisfactory moisture conditions. Fully developed larvae of *P. implicita* and *rugosa* required a temperature of 25° or

higher for pupation. Feeding of the larvae took place largely above 15°.

Temperatures below freezing destroyed many larvae, although some withstood at least — 4° C.

The free moisture content of the larvae comprised about 88 per cent of the total moisture content. Conditions under which the larvae had been kept did not materially affect their content of free moisture.

The length of the life cycle was dependent upon the physical ecological factors.

Adult Stage. The minimum limiting temperatures for the adults are dependent upon conditions, but correspond to the order of the spring emergence in the field. The maximum limiting temperatures were approximately 42° C. for the species studied.

First emergence depended upon the cumulative effects of heat, the optimum being near 25° for *P. implicita*. It was at a minimum at 14°, and was retarded at 30°. Daily emergence required a temperature of about 14° or higher at the soil surface for *P. implicita*, *anxia*, *fusca*, and *drakei*. *P. futilis* responded at a slightly lower temperature. Moisture had very little influence upon emergence in the field.

The optimum temperature for oviposition was about 25° for *P. implicita* and *anxia*, and about 20° for *P. futilis*. The moisture requirements were limited to between 28 and 58 per cent of soil moisture saturation.

May beetles apparently do not harden to withstand winter conditions. Temperatures below — 5° C. killed a majority of the beetles. The length of the exposure was very important. They were capable of maintaining a body temperature at least 9° above an environment that was only 4° above the killing point.

The free moisture content was approximately the same as found for the larvae.

Light intensity controlled the time of emergence in the evening and return to the soil in the morning under field conditions.

The beetles appeared to be independent of normal air pressure changes.

Wind, when strong, controlled the direction of flight and the place of feeding. Morning air currents, even when slight, controlled the direction of flight on the return to the soil.

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REVIEWS

SILVICULTURE ON AN ECOLOGICAL BASIS¹

This modern treatment of the whole field of silviculture on an ecological basis deserves to be known not only by the European and American student of practical forestry, but also by every ecologist, for its vast store of ecological data. Especially the teacher of ecology will be delighted with the experimental material condensed here to illustrate the many phases of plant relations to environment. It would be easy to find in this book examples of forestry investigations for every chapter in Weaver and Clement's "Plant Ecology."² The author is not only a leader in continental forestry, being Professor of Forestry at the Forestry School at Eberswalde, Germany, but a good botanist as well, with a wide practical experience in both fields.

The author gathers in one volume the work of hundreds of investigators in Europe, and, if his bibliography were not scattered throughout the whole book in the form of footnotes, it could serve as a welcome guide to the original investigators. The figures are mostly good photographs and well reproduced; the whole volume is pleasing in its appearance.

In the first part Dengler treats the forest as an ecological organism ("Lebensgemeinschaft") under the influence of the external and internal factors, *i.e.*, as a natural phenomenon. Eight chapters deal with the types of forest vegetation, the synecology and geography of forests, and their genesis. In the next seven chapters the influence of temperature, water, light, CO₂, wind, and soil on the forest and its tree-species is shown. Six more chapters contain the life cycles of forest trees, their autecology being well considered.

A second part of the book is given to man's interest in forests, as an object of culture, care, and profit. Here we find the economic forest types, and their make-up, discussed in six chapters. There follow nine chapters on reforestation and reproduction (artificial and natural), then the practical methods of silviculture (called "Bestandespflege"), the care of forests, in two chapters. The last three chapters offer a treatment of the various forms of forest management ("Betriebsformen"). A helpful index concludes this substantial volume.

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¹ Dengler, A. *Waldbau auf ökologischer Grundlage*. Ein Lehr—und Handbuch. 560 pp., with 247 figures in the text and two colored plates. Berlin, Julius Springer, 1930. Price, bound 39 RM. (German Marks.)

² Weaver, J. E., and Clements, F. E. *Plant ecology*. New York, McGraw-Hill Book Co., 1929.

KRAKATAO¹

The author at the beginning proffers two texts, singularly appropriate to the subject in hand. One is from Mark Twain:

"Whenever we have been furnished a fetish and have been taught to believe in it, and love it and worship it, and refrain from examining it, there is no evidence, howsoever clear and strong, that can persuade us to withdraw from it our loyalty and our devotion."

In selecting the other from the works of Treub himself, the author indulges in more than a trace of sarcasm:

"More than elsewhere, in a tropical country the botanist should exercise prudence and method in his researches. It is better, in this case, to be too sceptical rather than not sceptical enough."

Truly, Krakatao has become somewhat of a fetish. One of the recollections of my own early botanical training is a discourse, delivered by one known for accuracy and a sceptical turn of mind, on the invasion of new ground by vegetation in the tropics, as illustrated by Krakatao. I learned that in the eruption of August, 1883, every vestige of life upon the island was annihilated by the rain of hot volcanic ash, and the surface at the same time thoroughly sterilized by the same agency. I was told, further, that through the classic investigations of Treub, it had been shown that on such a sterile surface the first invaders are blue-green algae. These lowly organisms prepare the way for ferns, which for a time make a rich, dense growth, and which, in turn, render possible the establishment of the seed-plants—a sort of successional ontogenetic recapitulation of the phylogenetic story.

Treub visited the island three years after the eruption. Apparently his stay was limited to a single day, during which he investigated a small stretch of the shore and a minor portion of the adjoining interior. The author would seem to be amply justified in his contention that such a study was totally inadequate for the drawing of any general conclusions. He asserts, with apparent justice, that "it is unproven, not even rendered probable, that the original vegetation of Krakatao was totally destroyed by the eruption. In sheltered parts of localities which had *not* been covered with a *thick* layer of *hot* eruptive products and from where the covering layer soon disappeared . . . a number of plants may quite well have survived the eruption." (Italics by Backer.) The geologist Verbeek, visiting the island two months after the eruption, found the original soil in certain places already stripped bare of ash. Treub himself states that he saw from shipboard a number of plants near the summit of the cone. The height of this being 813 meters, these must have been of considerable size. Finally, no attempt was made to explore the upper portions of the island nor the eastern, southern and western

¹ Backer, C. A. The problem of Krakatao as seen by a botanist. 299 pp. Published by the author. For sale by Visser and Co., Weltevreden, Java; Martinus Nijhoff, The Hague, Holland. No date (1929-1930).

shores. Backer thinks that plants surviving in certain sheltered ravines near the summit may well have been responsible in part for the revegetation of the island. But, as he says:

"As it has not been proven that the original vegetation of Krakatao was totally destroyed by the eruption and, moreover, next to nothing is known of this vegetation, it cannot be established which plants after the eruption have been introduced, which not."

Treub made a real contribution, according to Backer, in noting the extensive thick covering of blue-green algae upon the sterile ash. Apparently these can exist with the minimum of nitrogen available in such places, and are to be considered as true pioneers. It is also admitted that this layer of organic material affords favorable conditions for the germination of fern spores. The remainder of the "succession" postulated by Treub is rejected by Backer as unproved and improbable.

Several parties have visited Krakatao since the historic expedition of Treub. As to the resulting publications, Backer remarks that "it has become a time-honoured custom to begin a paper on the new flora or fauna of Krakatao with stating something like that in 1883 'the island was completely devastated, stripped of all animal and vegetable life.'" Treub's conclusions, though almost entirely unsupported by any real evidence, have become incorporated in the fabric of scientific "knowledge." Accordingly, subsequent visitors have compiled lists of plants observed, for comparison with that of Treub, and have constructed hypotheses to explain how this and that species must have reached the island from more or less distant sources. Backer is rather hard on most of these explorers:

"Collecting some plants and vaguely speculating on them should, in the absence of all serious investigations, not be considered as identical with trying to solve ecological problems." With which sentiment we heartily agree.

Upon the methods of one of the more recent visitors, Dr. Docters van Leeuwen, he is particularly severe. It does not help the victim's case that a member of a scientific party visiting the island under his leadership "set fire to the dry grass in order to see whether it would burn. It *did* burn, to the great amusement of many present." In fact, it developed into a brush fire which swept a large part of the island. The incident is reminiscent of the similarly disastrous experiment of Robert Louis Stevenson in the pine woods of Monterey. We must, in justice to the author, note that he is equally severe upon himself for his earlier acceptance of Treub's conclusions:

"Often since I have severely blamed myself for that unpardonable levity."

Backer concludes his paper by comparing the literature of Krakatao to a "colossal skeleton brontosaurus some American author speaks of," reconstructed from the evidence of one small bone.

"I have tried to find the very few bones in these wagon-loads of rubbish and will finish by stating once more, that:

"1. It is not at all proven that by the eruption of 1883 all vegetable life on Krakatao was destroyed.

" 2. Even if this could be proven, we know with the exception of the littoral flora—*nothing at all* about the manner in which the new vegetation has appeared. Only guesses without scientific value have been made, but no reliable observations nor experiments.

" 3. Therefore the Krakatao-problem can neither now nor in the future either be posed or solved and is of no importance at all for Botanical Science."

Backer has apparently proved his case. It would seem that he might have done so more effectively in fifty pages than in three hundred—and we cannot suppress the intense desire to know what Dr. Docters van Leeuwen might say in reply.

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PROCEEDINGS

BUSINESS MEETINGS OF THE ECOLOGICAL SOCIETY OF AMERICA AT CLEVELAND, OHIO, DECEMBER 31, 1930 AND JANUARY 1, 1931

Meeting of December 31, 1930

The Society met at 5:00 P.M. with President Weaver in the chair.

COMMITTEE ON THE PRESERVATION AND STUDY OF NATURAL CONDITIONS IN PLANT AND ANIMAL COMMUNITIES

Dr. V. E. Shelford reported the plan for the work and organization of this committee, which was approved, as follows:

As organized at Des Moines, this committee combined two standing committees:

1. The Committee on the Preservation of Natural Conditions, which was established in 1917, prepared the Naturalist's Guide, and exerted pressure on government officials regarding several projects, notably the Glacier Bay National Monument, and

2. A committee composed of V. E. Shelford, W. P. Taylor and H. C. Oberholser, established in 1927 to encourage biotic study through the establishment of experiment stations and study centers.

It was found in the course of 1930 that several men in state or federal government service were among the most enthusiastic workers in the combined committee, but were either forbidden by law to lobby, or might readily be embarrassed by efforts of the chairman and secretary to influence government bureaus and legislative bodies. Hence *two* closely related committees with different personnel, except for temporarily having the same chairman, were authorized.

I. *Committee for the Study of Plant and Animal Communities*

Established in 1931. V. E. Shelford, Chairman (elected for 3 years).

This is a study committee. The name was agreed upon at a meeting of the committee on December 31, 1930. "Study" is used in the broadest sense to cover selection of areas and study of management, as well as scientific investigations. The committee is composed of a large number of persons in the following groups:

1. An Advisory Group of 20-40 members selected because of their wide knowledge either of *special fields* or of the communities of *particular regions*.¹ Their duty is to advise the officers of this committee, of the smaller committee or of the Society regarding the suitability of projects of all kinds. There are to be 2 or 3 members per region. The regions laid out were based upon the knowledge of the men selected, upon ecological unity of the region, and upon special reason.

- a. Regional Chairmen

The suggestion was made that some one man in the regional group should be chairman of the local representatives (see 2) in his region and be responsible for their organization and activities. The Society approved of the completion of the organization along these lines.

- b. Contributing Societies

The suggestion has come from The Wild Flower Preservation Society that CONTRIBUTING SOCIETIES be recognized on the basis of payment of \$1.00 per year (or more if desired) into the funds of the Ecological Society for the Committee. Since the Society's funds are very limited, the inducing of societies to do this would aid it greatly. The carrying out of this plan is contemplated as a part of the work of the regional chairmen.

- c. The Advisory and Regional Personnel

The complete list with date of expiration of service will be published later.

The chairman was authorized to arrange the terms of office of this group so that they expire in 1, 2, and 3 years, about one-third in each group. This will be published with the final personnel list.

2. Local (State and Provincial) Representatives

There are usually 2 in each state or province; most of those published in the Naturalist's Guide are still serving. The duties of the representatives include:

- a. The supplying of list of addresses of local societies interested in the conservation of nature, for the use of the chairman of committee II (see below) or other officers in legislative or other work.
- b. The making of contacts with influential citizens who may be persuaded to aid the Society's objects.

¹ It is understood that persons who are not members of the Society may serve on committees of this group, but should be urged to become associate members at \$1.00 per year.

- c. The encouraging of all local efforts looking toward the conservation of nature.

3. Chairmen and Members of Special Committees

About 15 special committees are contemplated to enquire into as many areas of national importance. Six of these deal with the reservation and study of *grassland*, 4 with *desert* and *semi-desert*, 4 with areas of special types of vegetation, and one with management of a game preserve. Since these will not all require urging before the same governmental body and will not all require action at the same time, as many committees as might seem necessary to chairman and advisory group were approved in order to save representative areas of neglected biotic types, such as grassland and desert. The plans and personnel of this group will be published later.

II. *Committees on the Preservation of Natural Conditions*

Two Legislative Committees, one for the United States and one for Canada. The one for the United States (II) was established with 5 members elected for 2 years:

V. E. Shelford, Chairman; G. D. Fuller, Secretary; Barrington Moore; A. R. Cann; A. G. Vestal.

(IIa) A committee of the same name for Canada was authorized, and the selection of personnel is in progress.

The resolutions appended originated in Committee II or were approved by it and passed by the Society.

V. E. SHELFORD, *Chairman*

NATIONAL PARKS ASSOCIATION

It was reported that the National Parks Association had selected V. E. Shelford as a trustee of that organization representing the Ecological Society. He was authorized by the Board of Directors to represent the Society in that capacity, and attended the organization meeting held in Washington on December 5, 1930. This action was approved by the Society.

NATURALISTS' GUIDE

The present status of the Naturalists' Guide was brought to the attention of the Society, and it was decided that a committee appointed by the chair should be authorized to negotiate a new contract with the publishers, if possible on the basis of a price of \$5.00 to the general public and \$4.00 (in lots of 5 or more) to members of the Ecological Society.

RESOLUTIONS

The following resolutions were passed:

Everglades Tropical National Park

The Ecological Society of America, a national organization of 600 members, devoted to the scientific study of nature, assembled in Cleveland in its fifteenth annual meeting, is dependent upon reservation of the original flora and fauna for the discovery of natural laws applicable to practical ends.

The Ecological Society of America is deeply interested in the proposed Everglades National Park and heartily approves of the preservation of the proposed area in an essentially natural condition. It constitutes a unique example of plant and animal life of great interest to scientists as well as to the general public. Much of the area has been little disturbed by man's activities and the Ecological Society recommends that the greater portion of it should be maintained in this primitive condition.

The two features which are of especial value and interest are the hammocks, especially those containing specimens of the *royal palm*, and the west coast mangroves. The hammocks are small, constituting the only examples of tropical jungle in the United States. They could be destroyed easily. Careful restrictions should be placed on their visitation, and these and all similar areas afforded adequate fire protection.

The coast mangroves exemplify the reclamation of land from the sea through the invasion of salt water by trees. The construction of a road along the west coast would seriously disturb the development of the mangroves by changing the circulation of the water, modifying the character of the vegetation, and disturbing the wild animal life. In the opinion of the Ecological Society this would ruin the western portion of the area as a natural reserve.

Both the hammocks and the mangroves are of national rather than local importance, and their preservation should be considered most carefully in the planning of roads to the extent of removing the proposed west coast road at least 30 miles inland for the reasons enumerated above.

The Ecological Society of America endorses the formation of the Everglades National Park provided the largest possible portion of it be preserved in its primitive wilderness condition, its value and its classification as a museum of nature and hence as a *National Park being dependent upon such preservation*. The boundaries of the proposed park should be so drawn as to exclude all railroad development.

Predatory Animal Control and Wild Life Research

The Ecological Society of America, a national organization of 600 members, devoted to the scientific study of nature and the application of natural laws to practical ends in grazing, agriculture, and forestry, assembled in Cleveland in its fifteenth annual meeting, is gravely concerned as to the re-

sults of the increase in appropriation for predatory mammal control involved in the ten year cooperative program of the Department of Agriculture represented by bills S. 3483 and H.R. 9599.

Part I. Predatory Animal Control

Whereas the Ecological Society of America does not oppose, but indeed favors such regulation and control of rodents and predatory mammals as impartial studies demonstrate to be necessary in the interest of the *general public*; and

Whereas the subject of the action of predatory animals in the destruction of range destroying rodents and other rapidly increasing herbivorous creatures, has been so little studied as to lay no adequate foundation for the past work or its proposed increases, and

Whereas the details of the control work to date have not been carried out by scientific men, and accordingly have been accompanied by so little direct scientific observation as to their effects on the life of the areas concerned that it constitutes no ground for confidence as to the results of extension; and

Whereas the ten year plan of the Department of Agriculture (see House Document 496) is based neither upon scientific investigation nor reliable data as regards the country as a whole, and appears not to recognize the great diversity of effects of poison campaigns in *different parts of* our country; and

Whereas the opportunities for corruption in illegal taking of skins is imminent in connection with this work in some localities;

Be it Resolved that the Ecological Society recommends that the proposed 10 year program be abandoned, and that necessary measures be enacted on the basis of the scientifically demonstrated needs of each particular locality.

Part II. Wild Life Research

Whereas, successful operations in the field of wild life management are dependent on a large adequate body of information and the results of research; and

Whereas, the responsibilities of the Biological Survey in the practical problems which confront it have been greatly increased, while its research activities have not been developed to anything like the same extent; these activities are absolutely essential to the safe application of regulatory measures in a field so difficult as wild life management; therefore

Be it resolved, that the Ecological Society of America does hereby go on record as strongly favoring the marked increase in the research functions of the Biological Survey, so that all its wild life activities may be conducted on a basis of science and intelligence, and with full regard for the interest of the general public; and be it further

Resolved, that the *Ecological Society of America* does hereby call upon all scientific organizations and the general public and Congress to support an adequate program of wild life research.

ECOLOGICAL MONOGRAPHS

Dr. A. S. Pearse reported the publication of Volume I, No. 1, of Ecological Monographs, of which copies were available for distribution.

COMMITTEE ON PUBLICATION OF LONGER PAPERS

The following report was presented and approved:

During the past year your committee has sponsored the publication of a paper by Ralph D. Bird on "Biotic Communities of the Aspen Park Land of Central Canada." The cost of extra pages and extra illustrations of this paper were defrayed in part from the funds contributed by sustaining members for the publication of longer papers.

The committee has also been active in the preliminary work which has led to the appearance of Volume I, Number 1, of Ecological Monographs. In view of the successful launching of this new series, devoted to the publication of longer papers in all fields of ecology, it seems that our committee appointed at the Nashville meeting (see *ECOLOGY*, Volume IX, p. 258) should now be discharged.

Respectfully submitted,

W. C. ALLEE, *Chairman*

The committee was discharged with an expression of thanks from the Society.

REPORT OF THE SECRETARY-TREASURER

The report of the Secretary-Treasurer was presented and approved as follows:

Receipts

Balance on hand, December 1, 1929		\$1,170.97
Dues		
Current (1930)	\$1,925.52	
Advance (1931)	442.00	
Arrears	69.00	
Sustaining (1930)	212.00	
Sustaining (1931)	96.00	2,744.52
Naturalists' Guide royalty		24.00
Interest		28.57
Dinner at Ames		17.50
Investments		
Certificate of Deposit	\$ 343.26	
Building and Loan	261.40	
Bush Service Corp.	500.00	1,104.66
Refund		6.00
Total receipts		\$5,096.22

Disbursements

ECOLOGY

Memberships	\$1,794.35	
Longer Papers Fund	765.52	\$2,559.87

Secretary's Office

Printing and Stationery	\$ 137.34	
Clerical Assistance	176.20	
Postage and Telegrams	15.36	
Expenses, Des Moines	81.45	
Expenses, Tucson	57.31	
Deposit box	2.00	469.66

Committee on the Preservation of Natural Conditions		187.49
Exchange and checks returned		12.08
Dinner at Ames		17.50

Total disbursements	\$3,246.66	
Balance	\$1,849.62	

Total Assets

General Fund

Cash on hand		\$1,059.65
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Life Membership Fund

Cash	\$ 789.97	
Securities	220.63	1,010.60

\$2,070.25

Membership

Sustaining Life	1	
Life and Sustaining	3	
Life	6	
Sustaining	84	
Institutional	4	
Annual	48c	
Associate	7	

Total paid up	585	
In arrears (2 years or less)	68	

Total	653	
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A. O. WEESE,
Secretary-Treasurer

AMENDMENTS TO CONSTITUTION

The Secretary reported that the proposed constitutional amendments published in *ECOLOGY* (11: 462, 1930) had been adopted by mail ballot.

The Society adjourned at 6:00 P.M.

REPORT OF THE BUSINESS MANAGER OF ECOLOGY

The following report of the Business Manager of *ECOLOGY* was presented and approved:

FOR THE FISCAL YEAR, DECEMBER 1, 1929–NOVEMBER 30, 1930

RECEIPTS AND DISBURSEMENTS

Received

Cash on hand (statement of 1929)	\$1,060.73
A. O. Weese, Treasurer, E. S. A.	1,794.35

Subscriptions	1,767.91	
Advertising	8.00	
Single copies and back volumes	579.30	
Cost of excess pages and authors payments	196.46	
Longer Paper Fund	765.52	
Postage	4.84	
Subsidy from Brooklyn Botanic Garden	300.00	
Interest to June 30, 1930, on deposit	9.20	
		<hr/> \$6,486.31

Disbursed

Printing

Lancaster Press, Inc. (October, 1929, reprints)	\$ 25.58	
January, 1930, issue	1,366.86	
April, 1930, issue	1,352.65	
July, 1930, issue	881.45	
October, 1930, issue	848.54	
		<hr/> \$4,475.08

Illustrating

National Engraving Co.	763.21	
Advertising	164.14	

Office expenses

Clerical assistant, 12 months at \$10.00	\$ 120.00	
1,000 subscription blanks	6.50	
Postage	72.50	
Loose-leaf sheets for cash book	1.75	
		<hr/> 200.75

Miscellaneous

Collection of charges on checks	\$.20	
Refunds on subscriptions	8.35	
Refunds on duplicate membership dues	6.00	
Purchase of back volumes	18.25	
Return of loan, B. B. G., 1929	646.33	
		<hr/> 679.13

Cash balance on hand	204.00	
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\$6,486.31

(Signed) C. STUART GAGER
Business Manager

Examined and found correct.

H. P. SCHOENBERNER

Auditor

ASSETS AND LIABILITIES

Assets

Cash in bank	\$204.00	
Bills Receivable		
Subscriptions (1929), Wheldon & Wesley	\$ 23.45	
Subscriptions (1930)	16.35	
Subscriptions (1931)	180.20	
		<hr/> \$220.00
Single numbers	8.81	
		<hr/> 228.81
		<hr/> \$432.81

Liabilities

Bills Payable	
Lancaster Press, Inc.	\$282.08
Advertising	4.00
Assets over liabilities	146.73
	<hr/> \$432.81

Circulation Data per Mailing List of October, 1930

1. Members	545
2. Subscribers	443
3. Exchanges	99
4. Advertisers	6
5. Editorial Office	2

1,095

Number of copies printed per issue—1,400.

Meeting of January 1, 1931

The Society met at 4:00 P.M. with President Weaver in the chair.

The following resolutions were presented by the chairman of the Committee on the Preservation and Study of Natural Conditions in Plant and Animal Communities, and approved by the Society:

Preservation of Hawks, Owls and Eagles

Whereas the Ecological Society of America views with concern the tendency throughout the country to slaughter hawks and owls because of supposed damage to poultry, game, and other birds; and

Whereas the Society feels that the people as a whole are insufficiently well acquainted with the species of hawks, owls and eagles to enable them to distinguish the harmful from the useful species; and

Whereas scientific investigation has shown that the vast majority of hawks and owls are of great positive value to agricultural interests in the broadest sense, and their destruction leads to greater and greater economic loss; therefore, be it

Resolved that the Ecological Society of America go on record as favoring the placing of hawks, owls and eagles on the list of birds protected by the state legislatures; and be it further

Resolved that the Society urge any and all organizations of sportsmen and conservationists to discourage the so-called "vermin killing campaigns" in which hawks and owls are killed, being convinced that such campaigns result in far greater harm than benefit.

Superior-Quetico Park

Whereas the Ecological Society of America recognizes in the Superior National Forest of Minnesota and the Quetico Provincial Park of Ontario, two adjacent areas in inestimable interest to the Society, to biological stu-

dents, and to the peoples of these United States and of the Dominion of Canada as a whole; and

Whereas the Society looks with grave uneasiness upon the repeated attempts at exploitation of these areas in the past, and with greater uneasiness toward possible future attempts because of the potential values of the natural resources therein contained in the form of water power, timber and fur, and

Whereas the Society believes that greater protection and greater efficiency lies in a consolidation of these two areas, with a mutual benefit to each; and

Whereas such a consolidation in the form of an International Park would stand as a monument to peace and good will between the peoples of these United States and of the Dominion of Canada; therefore be it

Resolved that the Ecological Society of America endorses the movement to unite the Superior National Forest of Minnesota and the Quetico, Provincial Park of Ontario, and urges the forwarding with all reasonable haste of all efforts toward the early consummation of such a consolidation.

Preservation of Whales

Whereas it is reported on good authority that more than 200,000 whales have been killed during the last ten years; and

Whereas whales have been commercially exterminated in one region after another until very few profitable whaling grounds now remain outside the Antarctic; and

Whereas the recent great increase in the number of floating whaling factories and the use of seaplanes for whale scouting now promise the speedy end of whaling; therefore

Be it resolved, that the members of the Ecological Society of America, assembled in their annual meeting of 1930 at Cleveland, Ohio, urge the adoption without delay of legislation, both national and international, of a character to perpetuate the species still extant and to preserve an adequate breeding stock of this valuable and interesting natural resource, and thus to insure the permanent continuance of the whaling industry.

*Series of Bioclimatic and Bioecological Stations*²

Whereas the University of Arizona and cooperating institutions (including the United States Forest Service, United States Biological Survey, Desert Laboratory of the Carnegie Institution of Washington and Boyce Thompson Southwestern Arboretum) are planning a series of bioclimatic and bioecological stations under different climatic conditions for the more adequate study of organism and environment; be it

Resolved that the Ecological Society of America does hereby express its appreciation of the attitude, interest, and activity of the institutions concerned, and pledges its approval of the project as planned.

² See Note at the end of this issue of Ecology.

Forest Natural Areas

Whereas the natural areas, primitive areas, wilderness areas, experimental forests and experimental ranges now being very wisely set aside by the United States Forest Service will afford increasingly important opportunity for scientific study through the years of the future; be it

Resolved that the Ecological Society of America hereby commends the Forest Service for its foresight in having these areas set aside, and suggests the need for making provision, through the Forest Service, Biological Survey, and other Bureaus concerned, for as complete as possible a scientific survey of the areas, including organic life and environmental conditions, at the time the areas are set aside or as soon as may be practicable.

Conservation of National Resources

Whereas inefficient conservation of our national resources of water, of soil fertility, of natural foods for fishes and wild fowl, are bringing enormous losses of these useful materials, and public money; and

Whereas these losses are reflected as a check upon prosperity on the farms, and in business, as a result of the wastage of water by floods, in the wastage of raw materials such as oil, sewage, and other by-products of civilization;

Be it resolved that the Ecological Society of America hereby places itself on record as favoring every well directed effort which may point out the factors involved in these wastages, and urges state and federal legislation and other measures which may decrease the wastage of water and promote the better distribution of water for serving its biologic uses, as well as its availability for power and for navigation: for preventing floods by control of run off waters before they become flood waters and to regulate the pollution of waters by the wastage into the public water courses of those substances which impair the broadest usefulness of a national water resource.

The Committee was authorized to expend between \$150 and \$200 during the year 1931.

COMMITTEE ON ECOLOGICAL NOMENCLATURE

The appointment of an Advisory Committee on Ecological Nomenclature by the chairman was authorized, the duties of the committee being defined as follows:

1. To ask that members report to the Committee any terms which seem to need interpretation or clarification.
2. To group these terms according to the types of workers chiefly using them.
3. To send these lists to the groups interested for discussion and return with comment and criticism.

4. To edit the replies from the groups and send to all members of the Society the complete list indicating the meanings which seem to have preponderance of support, with comments of the Committee.

COMMITTEE ON LAND UTILIZATION

The Society authorized the organization of a committee, with A. E. Waller as chairman, to form a clearing house for projects related to land and water utilization, to collect maps constructed on the basis of ecological surveys, etc. This committee is to report at the next meeting on the advisability of continuing the work on a large scale.

ELECTION OF OFFICERS

Officers for 1931 were elected as follows:

President, A. O. Weese

Vice President, Francis Ramaley

Secretary-Treasurer, A. E. Emerson

A resolution of appreciation to Western Reserve University, Case School of Applied Science, and the local committee was passed.

The meeting adjourned at 5:00 P.M.

A. O. WEESE, *Secretary*

NOTES AND COMMENT

SPONTANEOUS COMBUSTION IN THE MARSHES OF SOUTHERN LOUISIANA

On August 4, 1924, shortly before noon, while hiking in a dried marsh with a party of boy scouts, we observed the start of a fire which apparently ignited spontaneously. Our encampment was 2 miles east of Mandeville, Louisiana, at a point where the pine (*Pinus caribaea* and *P. taeda*) uplands, here interspersed with mixed hardwoods, touched the shore of Lake Pontchartrain. Stretching to the east of us, a strip of coastal marsh varying from zero at our encampment to nearly 3 miles in width some 6 miles distant, separates that sea level lake from the flat pine lands of slightly higher elevation to the northward. A narrow strip of cypress (*Taxodium distichum*), mostly dead, borders the pine, separating it from the marsh proper. The marsh vegetation consists chiefly of saw grass (*Cladium effusum*), cat-tails (mainly *Typha angustifolia*, although there are patches of *T. latifolia*), arrowheads (*Sagittaria* sp., probably chiefly *lanceifolia*), and sedges (mainly 3 or 4 species of *Scirpus*). There are also needle grass (*Juncus roemerianus*), marsh cane (*Phragmites communis*), Indian rice (*Zizania aquatica*), couch grass (*Spartina patens*), also at least 3 other species of *Spartina*, and one or more species of *Panicum*. The muck-like soil of the marsh, as rich as 90 per cent in combustible matter near the surface, varies from a few inches to several feet in depth. This rests upon an impervious alluvial clay stratum, which in turn lies upon the sandy strata of the coastal plain which are here below sea level. The soil of the adjacent low level pine barren type of country is also rich in humus, especially in the depressions.

We were in the midst of an unprecedented drouth, and the water level, which normally would stand a few inches above the grass roots, was several feet below the surface, all but a few deep lagoons and the bottom of alligator holes being without water. The impervious clay stratum completely prevents seepage of water from the adjacent sea level lake, which during that period averaged about 3 feet higher than the ground level in the marsh.

The temperature of nearby towns, as shown by the U. S. Weather Bureau, varied from 100° to 104° F., and was apparently the hottest spell of that summer in that part of the state. The sky was clear and in the sun the heat was so intense that it was impossible for the boys to walk barefooted in the sand. A strong southwest wind, estimated at 20 to 25 miles per hour was blowing across the lake from the direction of the Gulf of Mexico, and, although the relative humidity was not excessive at that time of the day, the actual amount of water vapor in the atmosphere at that temperature would naturally be considerable.

Except for a single crab fisherman who remained in the lake, we were the only human beings in that vicinity. My tent, being on the lake shore, commanded a view for several miles, there being no trees to the east between the lake shore and the border of the pine forest.

We were catching crabs and hiking along the lake shore when one of the boys called my attention to a column of smoke about a foot in diameter, rising from the marsh about $\frac{1}{8}$ of a mile in from the lake. We immediately ran to the fire to check it if possible and determine its origin, but, because of the nature of the combustible matter and the strength of the wind, it was already beyond control. As the partly dried marsh vegetation was not anywhere over 3 feet in height, no human could have been there without being seen.

Although not a single fire had been observed in the marsh or nearby pine woods prior to this date, and the lake shore was uninhabited for about 15 miles to the eastward, we

observed a number of large fires scattered over that area during that afternoon. During the late afternoon I drove by automobile to another scout camp near Slidell, about 18 miles east of our encampment. The highway runs through the pine woods at least 2 miles back of the marsh. I estimated at least a hundred fires along that 18 mile stretch, all between the highway and the lake and all in the uninhabited area in the marsh or



FIG. 1. Close-up of spontaneous marsh fire. Note cat-tails, grasses and sedges.

nearby flat pine lands. The scout executive at the other camp stated that they too had been fighting fires since noon, and that 3 fires started upon their camp grounds during the noon meal, one of them having burned up a tent before it was noticed. Prior to August 4, not a fire had been observed in that vicinity either; yet, if once ignited, fires would have spread and burned for weeks as they did following August 4th. For, while the pine lands here are under fire protection, it is not practical to check the marsh fires.

Regardless of the physical facts in the case, I cannot attribute such a large number of fires in such a wild, uninhabited area to accident or design by human agency. They were not along the lake shore, highways, or byways where one on foot, horseback or automobile would have been apt to set them. The region is dissected by a number of bayous mostly not navigable, all running in a north-south direction toward the lake. The fires were not along the shores of the bayous where one travelling by boat would be likely to set them. A single person could not have covered the territory, even upon horseback, in a day, and the nature and depth of the muck, with the occasional bayous, would make travel by horseback impractical if not impossible.

Looking at the physical facts in the case, we find existing at the time some of the same conditions which bring about the spontaneous heating and ignition of agricultural and industrial products, combined with such weather conditions as always accompany the

most disastrous forest and grass fires. Compared to the period prior to August 4, when no fires were observed, the temperature was hotter, the wind stronger and the barometer higher. The relative humidity readings at New Orleans, the nearest Weather Bureau

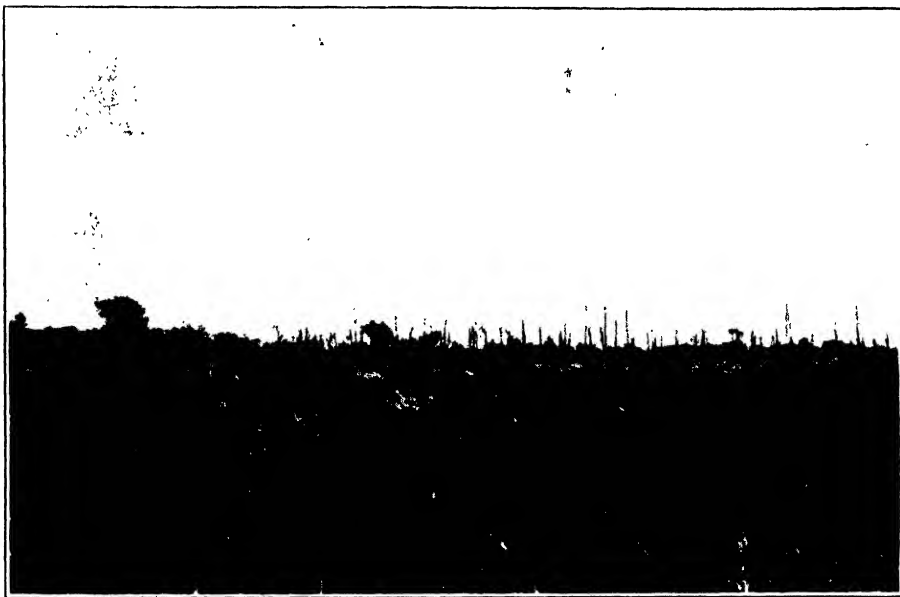


FIG. 2. Spontaneous marsh fire from $\frac{1}{4}$ mile. Note cat-tails, sagittarias, couch grass, etc. Dead cypress swamp (probably killed by salt water) in fire area. Living cypress in background to left, and beyond that pine flats. Lake Pontchartrain is behind the camera and to the right of picture.

station, show considerable vaporized water in the atmosphere on that date, much dryer periods having preceded the one in question. The weather bureau readings at New Orleans for the first week of August follow:

Date 1924	Barom- eter	Maxi- mum temper- ature	Rela- tive hu- midity 7 A.M.	Rela- tive hu- midity 12 noon	Precipitation 24 hr. period	Wind (maximum velocity and direction)	Wind (prevail- ing di- rection)
Aug. 1...	30.06	94° F.	80	58	0	13 mi. per hr. SW.	SW.
Aug. 2...	30.05	94 F.	72	49	0	14 " " " SW.	SW.
Aug. 3...	30.07	96 F.	81	50	0	12 " " " SW.	SW.
Aug. 4...	30.10	96 F.	75	55	trace	20 " " " W.	SW.
Aug. 5...	30.07	89 F.	73	61	trace	22 " " " SW.	SW.
Aug. 6...	30.03	92 F.	80	60	.12 inches	18 " " " SW.	SW.
Aug. 7...	30.04	92 F.	83	59	0	12 " " " SW.	SW.

The writer became interested in this phenomenon largely because of its ecological significance. While any speculations as to the causes of this apparent spontaneous ignition cannot be considered authoritative, they are nevertheless submitted as clues of an eye witness which might serve as guidance for someone better posted in the subject of spontaneous combustion.

My interpretation of the facts, then, is that the intense light and heat accelerated the normally slow oxidation of a finely divided, easily oxidized peaty material in which loss of heat by conduction would normally be very slow. The strong wind evidently penetrated the matted grass and humus sufficiently to furnish a generous supply of oxygen, but, being pre-heated, not only by the direct rays of the sun but by radiation from the marsh and possibly also by oxidation of gases rising from the marsh, could not conduct the heat away as fast as it generated. In addition to the probable formation of combustible gases developing in the humus, by what virtually amounted to a distillation in the presence of water vapor, there was no doubt much oxidizable unstable nitrogenous and carbonaceous matter, and perhaps even films of easily oxidizable vegetable oils, all distributed upon the surfaces of porous cellular materials. Further, the presence of abundant water vapor to act as a catalyzer, or reacting medium, perhaps interacting with molecular oxygen to produce hydrogen peroxide and atomic or active oxygen, must have been an important contributing factor. The principal difference that I can detect between these fires and fires in manure heaps or haystacks is that the initial heating which starts the accelerating oxidation process is not due to combustion alone or combined with a fermentation process, but to the heating by the direct sun's rays. The progressive evolution of heat may have occurred over considerable space as well as time, in contra-distinction from the phenomenon in a fire pocket in a haystack. That is, a layer of moving air in which the oxidation was taking place, may have gathered heat faster than it was dispelled in its progress over the surface of the marsh. The unstable unsaturated compounds which brought about the final ignition were very likely developed during the early stages of the heating from products laid down previously in the marsh under water and under anaerobic conditions.

That summer, similar rather sudden epidemics of fires occurred in muck soils in drained lands near my home in New Orleans. In one case I noticed what appeared to be a very small fire breaking out on the side of a stump in an empty lot, and I secured a bucket of water to extinguish it. It really took several buckets, for the fire had burned a large hole in the muck soil, and the condition of the under side of the cypress stump showed that it had been burning for some time in a partly smothered condition, and was only breaking through to the surface when observed. During a similar interval, a fire started with a match or cigarette would have set all the dried weeds and grass in the lot in flame and would not have burned the ground so deeply under the stump before spreading. Of course, because of the almost ever presence of people on the outskirts of New Orleans, I would have hesitated to attribute any of these fires to spontaneous ignition, had I not been an eye witness to the fire in the marsh near Mandeville on August 4th.

I have tried often to secure further evidence of similar spontaneous fires in nature. Trappers and rangers observing similar phenomena believe that fires sometimes travel under the surface for long distances, but this is impossible. The more combustible material is at the surface, and the clay subsoil is always damp.

Since 1924 the rainfall has been excessive in southeastern Louisiana, and, except for the grass fires set by trappers in the fall, there have been no epidemics of summer fires. With the summer drouth of 1930, the fires have been serious again in the same areas, although I was not as fortunate in securing as convincing evidence as in 1924.

PERCY VIOSCA, JR.

RESEARCH DEPARTMENT,
SOUTHERN BIOLOGICAL SUPPLY CO., INC.,
NEW ORLEANS, LA.

NOTES ON THE MARINE INVERTEBRATE FAUNA OF THE VIRGINIA CAPES

For the past few years I have been engaged in studies on the marine invertebrate fauna of the coast of New Jersey. In making these studies I have been rather impressed with the fact that so little is known concerning the fauna of our coast between Cape Cod and Cape Hatteras; consequently it was difficult to ascertain the exact distributional limits of many of the species collected in New Jersey waters. More recently I have become interested in some studies on the Pleistocene of the Atlantic Coastal Plain. Here again the lack of data on the exact distributional limits of marine species has made it difficult to compare the distribution of Pleistocene species with those of the present time.

The section of the coast between Cape May, New Jersey, and Cape Hatteras, North Carolina, seems to have been especially neglected. Among the few people who have reported on the fauna of this region are Henderson and Bartsch ('16) who recorded the marine mollusks from Chincoteague Island, Virginia, and Uhler (1878) who recorded a few notes on the fauna of Fort Woll, Virginia.

Because of the lack of information concerning the fauna of the "Del-Mar-Va Peninsula" a collecting trip was made to Cape Charles, Virginia, on June 16, 1929. A single day's collecting proved very profitable, and several new records were found. Because of the success of the first trip, the region was visited again on October 27, 1929. The autumn trip also proved interesting, and numerous animals were seen that had not been observed in the summer trip. On both of these trips I was accompanied by Mr. Ernest Mottershead who aided in the collecting. The third visit to the region was on February 8, 1930, when I spent part of a day collecting along the ocean beach at Virginia Beach, Virginia (near Cape Henry).

I am indebted to Dr. Waldo L. Schmitt, Dr. Mary J. Rathbun and Mr. Clarence Shoemaker of the United States National Museum and to Mr. E. G. Vanatta of the Academy of Natural Sciences of Philadelphia for help in the identification of certain species, and for information concerning geographical distribution.

NOTES ON THE FAUNA OF CAPE CHARLES

Mud flats

The mud flats along Chesapeake Bay near Old Plantation Creek were probably the best collecting grounds visited. Unless otherwise indicated the animals mentioned below were found on both the June and October visits. The most abundant mollusks were: *Arca campechiensis* and *Alectrion obsoleta*; the following were also found alive: *Pecten gibbus irradians*, *Columbella avara*, *Polinices duplicata* (June), *Alectrion vibex* (June) and *Melanella jamaccensis* on the Sea Cucumber *Thyone briareus* (October). As far as is known *M. jamaccensis* has been reported only from Florida and the West Indies.

The crabs *Callinectes sapidus*, *Ovalipes ocellatus* and *Libinia emarginata* were seen on the flats on both visits, and a dead specimen of *Limulus polyphemus* was found on the October visit.

An interesting find was a living specimen of the Serpent Star, *Ophioderma brevispina*, found between the tides on June 16, 1929. The worms *Nereis pelagica*, *N. limbata*, *Depraea rubra* (October) and *Diopatra cuprea* (June) were found burrowing in these flats and in similar flats near Cherrystone Inlet.

Rock jetties

On the numerous rock jetties near the town of Cape Charles were found the barnacles *Balanus balanoides* (first record south of New Jersey), *B. eberneus*, numerous oysters (*Ostrea virginica*) living between the tides, and other mollusks: *Modiola demissus*, *Columbella avara*, *Urosalpinx cinerea*, *Eupleura caudata* (June), *Anomia simplex* and *Littorina irrorata* (October); sea anemones *Sagartia luciae* and *Cylista leucolena*; numerous

large isopods, *Lygida exotica* and some small springtails *Anurida maritima* (June). This, and an unpublished record (U. S. Nat. Mus.) from Hog Island, Virginia, mark the northern limit of *L. exotica*.

In the sand at the base of the rocks *Alectrion obsoleta* was abundant.

Wharves

On the sand by the "Plank Bridge" were numerous crabs; *Panopeus herbstii*, *Eurypanopeus depressus*, *Uca pugilator* and especially *Sesarma reticulata*. In the shallow water not far away were noted *Callinectes sapidus*, *Ovalipes occellatus* and *Arenarius cribrus*.

Tide pools along beach

Small tide pools along the beach proved to be the home of the crabs: *Neopanope texana sayi* (October), *Pagurus longicarpus*, *Callinectes sapidus*, *Clibanarius vittatus* (October) (northern limit), *Ovalipes occellatus*; the shrimp *Palaeomonetes vulgaris*, *Crangon packardii* (October) (northern limit), *Crago septemspinus*; the young isopod *Exosphaeroma* sp. (October) and the amphipods *Melita fresnillii* (October), *M. palmata* (October), *M. nitida* (October), *Elasmopus pocillimanus* (October), *Carinogammarus mucronatus* (June), *Corophium cylindricum* (October). The small clam *Gemma gemma* was found in the sand in some pools.

Beach

Numerous pieces of eel grass (*Zostera marina*) were found stranded in the beach; on these were noted some hydroids (*Obelia* sp.) and the bryozoa *Bugula turrita*, *Crisia eburnea* and *Membranipora monostachys* (June). On October 27, 1929, one piece of eel grass was covered with young barnacles which Dr. H. A. Pilsbry tells me is probably the rare *Chthamalus fragilis*.

In the sand above high tide were found the amphipod *Talorchestia longicarpus* and the oligocheate worm *Pontodrilus bermudensis*.¹ Cast on the beach were numerous shells. The following in addition to those already mentioned were conspicuous: *Alectrion trivittata*, *Fulgur carica*, *F. canaliculata*, *Crepidula fornicata*, *C. plana*, *C. convexa*, *Venus mercenaria*, *V. campechiensis*, *Petricola pholadiformis*, *Ensis directus*, *Tagellus gibbus*, *T. divisus*, *Cardium mortoni* and *Tellina tenera*. Tubes of the worm *Eupomotus dianthus* and numerous sponges, *Microciona prolifera*, *Halichondria panicea*, and other unidentified species, and stranded medusae, *Aurelia flavidula* (October) and *Cyanea arctica* (October) were also on the beach. The fleshy bryozoan *Alcromidium varelli* was very conspicuous.

NOTES ON THE FAUNA OF CAPE HENRY

Not very much of interest was found on the visit to Virginia Beach on February 10, 1930. The sandy beach at this locality was not a very favorable habitat for many marine species. The only item worthy of note was the presence of a very great number of young starfish, *Asterias forbesii*, found cast on the beach together with shells of common mollusks. The presence of young starfish at this season of the year, while not unheard of, does, I believe, deserve mention.

LITERATURE CITED

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¹ "So far as I recall this species has not been reported so far north though I found it common years ago in Florida and Georgia." Dr. J. P. Moore—personal communication to the writer.

NOTE: Since this note was accepted for publication Dr. R. P. Cowles' extensive "Biological Study of the Offshore Waters of Chesapeake Bay" has appeared. (*Bull. Bur. of Fish.*, 46: 1930.) As Dr. Cowles' report is concerned especially with the offshore waters and not with the littoral zone, it is thought advisable to publish the present note.

A SIMPLE EVAPORIMETER AND SOME DATA OBTAINED BY ITS USE IN THE CANAL ZONE

One of the workers at the Barro Colorado (Canal Zone) laboratory of the Institute for Tropical Research desired data concerning the relative rates of evaporation at a number of places in the vicinity of the laboratory. There was not time to get a supply of the standard evaporimeters and, accordingly, the following method, which seemed to work very well, was devised.

Essentially, it consists of an evaporating surface kept constantly moist by drawing water from a test-tube through a wick.

After some experimenting it was found that the best of the available materials for the wick and evaporating surface was a fabric commonly sold under the trade-name of Kotex. However, since this material has little tensile strength when wet, it was covered with thin, coarse-meshed cheese-cloth stitched here and there to hold the two together.

A wire frame, shaped like an outstretched flag on a flag-pole, was made (Fig. 1). The absorbent material was cut into a similar shape, but with the "flag" somewhat smaller than that of the wire frame. The two were then fastened together with thread. Since the fabric flag was somewhat smaller than the wire one, the two did not actually touch, thus avoiding undesirable rust on the evaporating surface. An abundance of rust was further avoided by the use of galvanized wire.

The "flag-pole" was made of such a length that when its lower end rested on the bottom of the test-tube the flag came about a centimeter above the test-tube's rim. The object of making the device in the shape of a flag was to allow the evaporating surface to swing in any reasonably strong wind so that the wind would sweep across, instead of against, the evaporating surface. This also made for uniformity of exposure in shifting winds.

As used in these experiments, the fabric flag was $4 \times 3\frac{1}{2}$ cms. The wick, which was a continuation of the flag, was about a centimeter wide and long enough to reach nearly to the bottom of the test-tube. Since the bottom of the flag was about a centimeter above the rim of the test-tube, a square centimeter of the wick was also an evaporating surface. This gave a total of 15 square centimeters of fabric but, since both sides of it evaporated, there was a total of 30 square centimeters of evaporating surface.

An outer wire frame was made, as shown in figure 1, to be hung from a branch or other support. The test-tube was fastened inside the frame, and was there protected from being hit by swaying twigs. The frame had a roof of table oilcloth to shield the evaporating surface and the test-tube from rain, also from mid-day sun.

Reading the amount of evaporation was simple. After the fabric had been saturated with water, it, with its wire support, was put in place. Then the tube was filled with water to a marked height near its top. As water was evaporated from the flag it was automatically replaced by absorption through the wick from the tube. When a reading was desired, the tube was refilled to the mark, and a notation was made of the amount of water required to do this. That was the amount of water evaporated. It is well to make the readings frequently enough to avoid using up a large part of the water from the tube. Otherwise the wick must raise the water so far that the flag may not be kept uniformly moist.

It is clear that one of these evaporimeters is not directly comparable with another unless each be made exactly alike in all of the essential details. Since this is not feasible, the various ones must be calibrated. To do this with the set of 9 which we made at Barro

Colorado, they were run side by side for a number of days. The one which gave readings most nearly the average was taken as the standard, and multiplying factors were calculated for the others. All 9 were so similar that the factors ranged only from 0.90 to 1.14.

To reduce still more any errors due to individual differences, the evaporimeters were changed from station to station at each reading. Consequently, we felt that we could in this way secure rather reliable data concerning the relative rates of evaporation at each

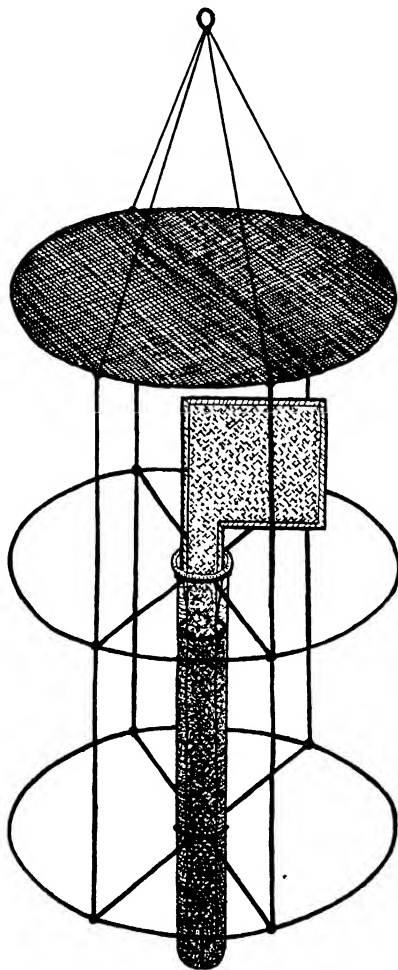


FIG. 1. The evaporimeter, showing the flag surrounded by the wire frame, and the wick in the test tube. The sketch also shows the outer wire frame for holding the evaporimeter, and the cover for protection against rain and mid-day sun.

station. Of course, such data are not directly comparable with data secured by other types of evaporimeters, and they can not be very accurately translated into other terms such as relative humidity.

The following data, which were obtained merely to try out the device, show the general type of results which may be expected. It is left for the other worker to report on his problem.

Near the laboratory there is the Chapman House set on tall posts. The laboratory's meteorological instruments, including a recording hygrograph, were located under the shelter of this cottage. The average daily evaporation-rate obtained by the evaporimeter described in this note was 3.84 cc. at this place for the last two weeks in November (the end of the rainy season). The average relative humidity, based on bi-hourly readings of the hygrograph record, was 87 per cent.

A few meters from this cottage is the sand-box tree which was an important part of Allee's studies (1926, *Ecology*, Vol. VII, pp. 273-302). We fastened a pulley to a branch of this tree. By means of a rope through this pulley an evaporimeter was easily raised to 16 meters above the ground, and lowered when a reading was to be made. In the same way, data concerning the evaporation rate 8 meters above the ground at this place were obtained. A third instrument was placed among the bushes at the base of the tree. The highest instrument was just under the forest canopy, and during the last two weeks of November the average daily evaporation rate was 5.76 cc. The comparable rate at mid-distance was 4.96 cc., and at the foot of the tree it was 2.08 cc., the ratios being 2.8:2.4:1.0.

Owing to an enlargement of the laboratory clearing, this tree is now near the edge of instead of in the forest, as it was when Allee did his work there. Furthermore, Allee's measurements were made near the end of the dry season (March) instead of at the end of the rainy season (November). He used two Jules Richard recording evaporimeters. One was located in this sand-box tree at a height of about 23 meters. Of his instruments and the placing of the lower one he said (p. 281): "Both the upper and lower instruments were protected from possible rain and the upper one from direct sunlight and wind by canvas shelters which also served to reduce the air movement somewhat. In order to secure maximum evaporation at the lower level this cover was removed at the beginning of the second week and after two days the instrument was placed on a stump at some distance from any large tree. The evaporation rate was not markedly affected by these changes." Air movement is such an important factor in natural evaporation that there is some objection to interfering with it. The same might be said of the effect of direct solar radiation, but it is not easy to admit it near noon and at the same time guard against possible rain.

Allee found that the evaporation rate under the conditions of his observations at about 1 meter was to that at about 23 meters above the ground as 1.0 to 2.1. The data presented here show that the rate at 1 meter was to that at 16 meters as 1.0 to 2.8. Since the 16-meters height was still below the forest canopy, and the 23-meters height was near its top where evaporation is undoubtedly greater, the difference in the ratios is in the opposite direction from expectation. There are a number of possible explanations. One is that Doctor Allee's interference with free movement of air about his evaporimeter (especially about the upper one?) tended to mask the really more extreme difference between his two stations. Another is that our ground station, being actually at the foot of the tree and surrounded by other growth was more sheltered than his, which was "at some distance from any large tree." A possible and more interesting explanation is that there may be a real difference due to the difference of seasons. Thus, during the rainy season the ground is fully saturated, resulting in much humidity and little evaporation near its surface; but in the dry season (Allee's data) the ground is not saturated, evaporation is relatively greater, and so the ratio between it and even the top of the forest canopy is less than that (1:2.4) between the rainy-season ratio near the ground and that only 8 meters above the ground.

A few meters still farther into the forest there is a small clearing where Mr. Zetek is conducting experiments with termites. We hung one of our evaporimeters on a bush at the edge of this clearing and found an average daily evaporation rate of 2.34 cc. This, compared with the 2.08 rate at the foot of the Allee tree a few meters distant, but sur-

rounded by undergrowth on all sides, serves as an indication of the effect of such undergrowth, although it is not exact because the "Termite Yard," while small and entirely surrounded by forest, had been cleared of trees as well as of undergrowth.

Two interesting stations were: one along the F. E. L. trail in a forested ravine, and another about 50 meters distant at the Shannon House on the cleared slope fully exposed to the sweep of winds and to the drying effect of sun, although the instrument itself was shaded. At the former station the average daily evaporation rate was only 1.31 cc.; at the latter it was 5.60 cc.

It is somewhat surprising that the exposed hillside station had the same evaporation rate as (actually but not significantly less than) the one in the forest canopy (5.76 cc. per day). A possible explanation is that the former, being much nearer the level of Gatun Lake, was more affected by moisture from the lake. I do not have an exact measurement of the altitude of the Shannon House, but an estimate of 15 meters above the lake may be sufficiently accurate for the present purpose. Allee stated that the base of his tree is "about 135 feet above Gatun Lake." Since our upper instrument was 16 meters above this base, it was about 41 meters above the lake. This difference of about 25 meters in elevation above the lake's surface may well explain the similarity of rates in the higher forest canopy and the lower exposed station. The fact that altitude above the lake may be an important factor is further indicated by a short (6 days) series of readings near the ground in the forest where the F. E. L. trail joins the S.-M. trail. This is near to but possibly 10 meters higher than the base of the Allee tree (2.08 cc. per day) and the Termite Yard (2.34 cc. per day). The situation, being where two trails join, is more open than the former, but not nearly so exposed as the Termite Yard; yet its average daily evaporation rate was 2.63 cc., an increase which I can explain only by saying that it was somewhat farther above the moisture from the lake.

If evaporation rate is of any importance in the distribution of organisms, the marked difference in the rate at the Shannon House (5.60 cc.) and that only 50 meters distant and at roughly the same altitude but in a ravine (1.31 cc.) is significant. The latter measurements were made somewhat more than a meter above the ground at a relatively open place along the trail and well above the bottom of the ravine where there is a small stream. The evaporation close to the stream was so small that it did not seem worth measuring. This marked difference in so short a distance may go far toward explaining the differences in the animal and plant life at the two places.

SUMMARY

A simple, inexpensive, and easily made evaporimeter is described and examples of its use in the Canal Zone are given.

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THE DRAGOYLE AS AN ECOLOGICAL INSTRUMENT¹

Under the name of gargoyle, the senior author called attention (Science, 70: 148) to the possible use of this instrument. Since that time the Dragoyle Company, Newark, New Jersey, has put out some of the instruments under the name of dragoyle. The data upon which this paper is based was obtained with some of these instruments during the summer of 1930 in the vicinity of the University of Michigan Biological Station on Douglas Lake, Cheboygan County, Michigan.

¹ Contribution No. 313 from the Department of Botany, Kansas State Agricultural College, and a contribution from the Biological Station of the University of Michigan. Gleason, H. A. The structure of the maple-beech association in northern Michigan. *papers Mich. Acad. Sci., Arts, and Letters*, 4: 285-296. 1924.

The dragoyle (Fig. 1) consists of a glass tube conspicuously enlarged at one end to look like a head, while the other end is slightly enlarged to resemble the tip of a tongue. After the bulbs are blown, about one cc. of colored liquid is introduced, the instrument is partially exhausted, and sealed off. The large bulb or head is covered with a cloth, the ends of which have been brought together and tied to form a wick that extends down into a reservoir of water. In operation the instrument is held with the tube slanting downward about 40° . As the water evaporates from around the larger bulb,

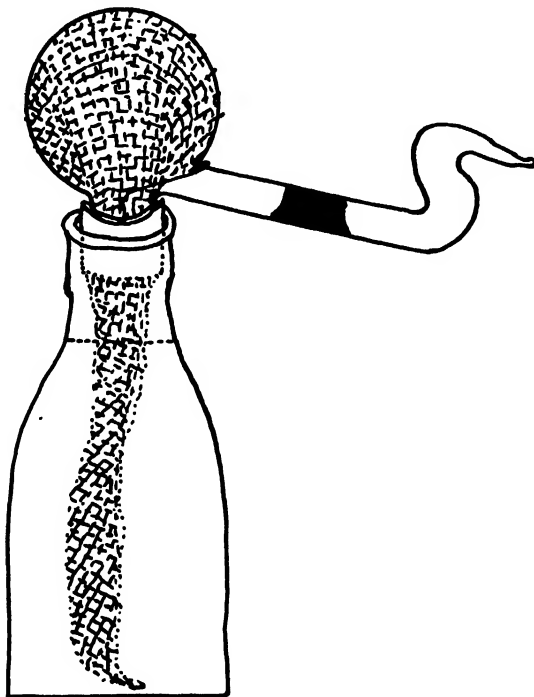


FIG. 1. Sketch of dragoyle, showing the larger of the two glass bulbs covered with cloth leading down through a loose rubber sleeve into a reservoir of water. The drop of colored liquid is about midway between the two heads, or half way to a "beat." A stiff wire holds the glass part in position above the rubber sleeve.

it cools the air within, which is then under less pressure than that in the smaller bulb. Under these conditions the liquid seal is pushed up into the larger bulb. An immediate equalization of temperature and pressure conditions takes place, and the liquid flows down the lower side of the tube to re-form a seal at the lower end of the tube. Continued evaporation makes a series of passages of liquid or "beats." Recording the number of beats per minute in various places gives the data to be obtained with the dragoyle.

For comparative results with a single instrument, standardization is not necessary, but the instruments may readily be standardized with each other, and in comparison with standardized atmometers. For the half dozen instruments at hand the relative rates were 100, 107.4, 100, 115, 104.1, and 122.6. Dragoyle No. 1 was compared with a standardized white spherical Livingston atmometer 121 times, each time taking count of the number of beats while the atmometer was evaporating 0.1 cc. (corrected 0.079 cc.). As a result of this comparison it was found that each dragoyle beat was equivalent to an evaporation of 0.0006081 cc.

In operation, the dragoyle, a watch (and a thermometer) are held in one hand in the position desired, while a counter is operated in the other hand. An assistant to record the data adds greatly to the ease and volume of experimentation.² In moving from station to station it is best to allow the instrument to work a minute or two before taking

TABLE I. *Comparative evaporation around plants as individuals (beats per minute), obtained from dragoyle readings*

Plants	Ground	Crown	1 m. above ground, outside of foliage	1 m. above ground, inside of foliage	2 m. above ground, inside of foliage	Cases	Habitat
<i>Acer saccharum</i>	24	—	—	30	33	25	forest
<i>Ammophila arenaria</i>	54	61	—	—	—	8	sand dune
<i>Aralia nudicaulis</i>	26	36	—	—	—	14	aspens
<i>Asclepias syriaca</i>	46	58	—	—	—	15	meadow
<i>Aspidium spinulosum</i>	41	46	—	—	—	4	forest
<i>Betula glandulosa</i>	40	82	—	—	—	4	bog
<i>Betula papyrifera</i>	—	—	49	42	—	26	aspens
<i>Calamagrostis canadensis</i>	14	49	—	—	—	9	wet meadow
<i>Calamovilfa longifolia</i>	60	64	—	—	—	5	sand dune
<i>Carex lasiocarpa</i>	32	59	—	—	—	11	bog
<i>Chamaedaphne calyculata</i>	27	49	—	—	—	23	bog
<i>Cornus stolonifera</i>	—	—	64	60	—	14	sand
<i>Eleocharis palustris</i>	26	59	—	—	—	7	marsh
<i>Fagus grandifolia</i>	37	—	—	43	47	14	forest
<i>Larix laricina</i>	26	—	—	46	57	22	bog
<i>Nymphaea americana</i>	49	—	—	—	—	9	aquatic
<i>Pinus banksiana</i>	52	—	—	64	68	18	Jack Pine
<i>Pinus resinosa</i>	67	—	—	74	81	16	forest
							second growth pine
<i>Populus grandidentata</i>	—	—	51	46	—	28	aspens
<i>Populus tremuloides</i>	—	—	51	51	—	14	aspens
<i>Prunus pennsylvanica</i>	—	—	57	56	—	12	aspens
<i>Pteris aquilina</i>	39	41	—	—	—	35	aspens
<i>Quercus borealis</i>	—	—	49	44	—	26	aspens
<i>Sarracenia purpurea</i>	23	60	—	—	—	6	bog
<i>Scirpus americanus</i>	47	61	—	—	—	7	aquatic
<i>Scirpus validus</i>	43	65	—	—	—	16	aquatic
<i>Spartina michauxiana</i>	27	55	—	—	—	9	beach
<i>Thuja occidentalis</i>	24	—	—	41	44	50	Thuja forest
<i>Trifolium pratense</i>	43	57	—	—	—	8	meadow
<i>Typha latifolia</i>	21	56	—	—	—	14	marsh

² For such assistance the authors are greatly indebted to Mrs. R. L. Black.

readings. One must be sure that water is coming up the wick as fast as necessary. At first in some of the instruments the rubber neck fitted sufficiently tightly to partially stopper the bottle and diminish the rate of flow of water up the wick, making the instrument work very erratically. The head may be rinsed occasionally or brushed with a toothbrush to keep it clean.

The dragoyle is very sensitive to slight changes in the evaporating conditions of the air, and responds quickly to differences in air motion, temperature, humidity, and sunshine. It can be very easily moved about with a minimum of trouble, and thus a large number of readings from different places may be obtained quickly. Its record, however, is lost as soon as made unless one records it or measures the amount of water lost from the bottle. A continuous record would involve a great deal of close attention, and would no doubt be better obtained from the Livingston atmometer. The particular advantage of the dragoyle over the atmometer is that records can be obtained more quickly and in more different places with a single dragoyle; while the atmometer is a superior instrument for the recording of total evaporation in longer continuous units of time.

Field work was taken up under two headings. Seven characteristic areas were selected, exhibiting varying habitats in each of which from 2 to 7 substations were located. The habitats included open and dense aspen areas, *Carex lasiocarpa*, *Larix* and *Thuja* bogs, second growth pine and the maple-beech forest. No descriptions of these areas need be given here as they have already been treated at length.³ A dragoyle was

TABLE II. *Comparative evaporation around plants by associations (beats per minute), obtained from dragoyle readings*

Association or groups of associations	Ground	Crown	1 m. above ground, outside of foliage	1 m. above ground, inside of foliage	2 m. above ground, inside of foliage	Cases
Aquatic						
Open water	47	—				11
Others	31	55				81
Aspens						
Ground plants	37	41				67
Trees	—	—	51	48		110
Bogs						
Ground plants						
Open water	47	—				11
Mat plants	28	53				75
Shrubs	42	55				15
Shrubs	—	—	62	58		27
Trees						
Larix	26	—	—	46	57	22
Thuja	24	—	—	41	44	50
Dunes						
Ground plants	62	67				35
Jack Pine plains						
Ground plants	51	63				3
Trees	52	—	—	64	68	18
Trees	—	—	69	69		8
Norway Pine						
Trees	67	—	—	74	81	16
Maple-Beech forest						
Ground plants	30	40				28
Trees	32	—	—	44	49	56

³ Gates, F. C. Plant successions about Douglas Lake, Cheboygan County, Michigan. *Bot. Gaz.*, 82: 170-182. 1926.

operated in and near certain plants in each area in turn at least once a week throughout the summer. In addition to readings at these definite stations, readings were obtained from the vicinity of about 60 species of plants in various situations, and some readings without regard to plants.

Reference to Tables I and II will give a good idea of several of the points that may be found out with a dragoyle. A curve of rates obtained at intervals of a few days throughout the summer is similar to that which one would get from experimentation with a Livingston atmometer, and so is not reproduced here. Inspection of the entire collection of data brings out the points that: (1) evaporation in the foliage increases with height from the ground, while the temperature decreases; (2) evaporation is higher outside the foliage than within it; (3) the amount of evaporation around plants in any position in a given station on a given day is fairly steady, but varies greatly from day to day with the changes of weather; (4) miscellaneous height readings taken without reference to plants show a lack of uniformity when compared with those taken in the vicinity of plants; (5) rates of evaporation near the ground vary with different associations.

SUMMARY

The dragoyle is shown to be a useful ecological instrument for obtaining quickly and easily a quantity of data relative to the evaporation in the vicinity of plants as individuals and in associations.

The data lead to the same conclusions as from other instruments measuring evaporation.

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CONFERENCE ON WILD LIFE, FOREST, AND RANGE PROBLEMS

On April 26, 1930, the Conference on Wild Life, Forest and Range Problems met in Tucson, under the chairmanship of President H. L. Shantz of the University of Arizona. The interest in these problems, and in the effort to bring about a joint attack on them from all possible angles, is strikingly shown by the large attendance and number of groups which participated. There were representatives of no less than five Bureaus of the Federal Government, namely, the Biological Survey, Forest Service, National Parks Service, Indian Service and Bureau of Entomology; of nine educational and scientific institutions, the University of Arizona, University of New Mexico, State College of New Mexico, University of California, University of Colorado, University of Oklahoma, University of Pennsylvania, Carnegie Institution of Washington, and Boyce Thompson Southwestern Arboretum; of the States of Arizona and New Mexico; and of the Arizona Cattlegrowers Association, Arizona Game Protective Association, and New Mexico Game Protective Association.

The Chairman presented an outline for the establishment and maintenance of Climatic and Biological Stations, to be financed cooperatively and located in the principal biological types. The standard basic equipment was listed for measuring climatic factors, including air temperature, light, humidity, air movement, precipitation, evaporation, and transpiration; soil factors, including moisture, temperature, and texture; and for plant and animal observations.

The conference was divided into three committees, covering Wild Life, Forests, and Range, under the chairmanship, respectively, of Walter P. Taylor, G. A. Pearson, and W. G. McGinnies. Each of these committees met, and, in the afternoon session, presented its report. All endorsed the formation of the Climatic and Biological Stations,

and made various suggestions. A fourth committee, on Water Conservation and Erosion, was provided for, under the chairmanship of C. K. Cooperrider, and is now in process of appointment.

The Conference marks the beginning of an organized effort to utilize the combined facilities of the biological sciences and engineering in solving the more important problems involved in the conservation and wise utilization of the organic natural resources of a vast territory. It is not without significance that the Ecological Society should be strongly represented, and that the program should be worked out from the ecological point of view.

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SOME CONCEPTS OF BIOECOLOGY¹

V. E. SHELFORD

I. INTRODUCTION

The term ecology should and does, to perhaps half of the interested individuals, convey the idea otherwise expressed by bioecology. It is true also that various lines of development of plant ecology have led quite away from any such ideal or idea as is expressed by bioecology. Certain plant ecologists have desired to learn the ultimate climax of vegetation with the obviously influent large animals (or their equivalents in domestic animals) excluded by fencing rather than reduced to their pristine numbers. The less obvious influents such as insects, other invertebrates, and even small rodents have not ordinarily been kept out. The resulting vegetation has been regarded as an expression of the relation of vegetation to climate. Such experiments are important, and, while possibly they have led to no very seriously erroneous conclusions from the standpoint of bioecology, they are, nevertheless, incomplete.

It is important to consider the fundamental concepts of those (some plant ecologists) who appear to believe that the vegetation is to be considered and named apart from the animals. One of these groups holds that the animals of a community are to be treated on a par with physiographic forces, etc. (Tansley, '29) and that the biotic community is not a unit as is the vegetation which makes up the plant part of it. Another group considers that it might be desirable to treat plants and animals together, but that this is impossible (Cooper, '26, '27). More often one hears plant ecologists referring to "our science," "our concepts," etc., while the vegetation is treated alone and no mention is made of animals, either on a par with physiography or anything else.

Weaver and Clements ('29) hold that *food* rather than physical factors, controls animals, and, since plants are the direct or indirect food of all animals, the biotic community has unity through food relations. The unity

¹ Presented before the Ecological Society of America in Des Moines, Iowa, Dec. 1929. Contribution from the Zoological Laboratory of the University of Illinois, No. 401.

of the plant-animal community was stated by the writer in 1912*a*. This idea was clearly elaborated by Vestal in 1914*b*, who wrote (p. 430): ". . . The relations between the assemblage of plants and the assemblage of animals are intimate and regular of occurrence; so much so that (1) the two are coextensive, (2) the two constitute together a community which may be called a biotic association,² (3) neither plant nor animal assemblage usually occurs independently of the other, (4) the geographic distribution of many of the plant and animal species which make up the assemblages are in general correspondence, (5) the species composition of the association, over its range, varies no more widely, relatively speaking, than would an assemblage of plants alone. Perhaps the single view-point of the botanist, on one hand, and the zoologist, on the other, has tended to a neglect of the dual character of the one problem. . . ."

It is the purpose of this paper to re-state the unity of the plant-animal community (which probably most ecologists will admit academically), and to suggest several principles which make such a concept tenable. Some of these are:

1. That because the larger and more influent animals tend to range throughout units of largest (formational) size including their seral stages, the biome or biotic formation is the natural ecological unit with some properties which are well illustrated by comparison with an organism.
2. That a much broader and more flexible view of controlling factors is tenable than the one which holds that the animals are merely an environmental factor acting upon plants.
3. That food relations, especially of abundant and influent animals, are usually flexible and rarely if ever obligate; and that observation of apparently restricted food relations made in one locality may not hold good under other conditions.
4. That the climaxes of nature (bioecological climax) include that vegetation which occurs with the pristine numbers and kinds of animals present.

II. THE FUNDAMENTAL UNIT OF ECOLOGY AND ITS CHARACTERISTICS

The fundamental units of ecology are the largest units, *i.e.*, those of formational rank (Anglo-American sense, or Vegetation regional rank (Du Rietz, '29) (see Brehm, '96 and Clements, '21)). They include all the developmental stages. This is necessitated by the habits of large influent animals (mammals and birds) which range over the climaxes and subclimax stages, often including also many very early seral stages.

It is an old practice to liken organisms to cosmic systems, and cosmic systems to organisms. Again in this case, it is convenient to liken the biome (plant-animal formation) to an amoeboid organism, a unit of parts, growing, moving, and manifesting internal processes which may be likened to metabolism, locomotion, etc., in an organism.

² Association is here used in the sense of community.

1. *Interaction Comparable to Metabolism.*

Food interrelations of animals serve to illustrate interaction (Fig. 2) which we may call processes comparable to metabolism. The actual processes in a deciduous forest community are little known, but to illustrate the general principles some disturbance may be assumed and discussed on the basis of such knowledge as exists (see Fig. 1). One of the outstanding facts is the increase of the deer accompanying the destruction of wolves, foxes, etc., by early settlers in Illinois. Wood ('10) depicts a continuous decrease in wolves and wildcats from the beginning of settlement to their practical

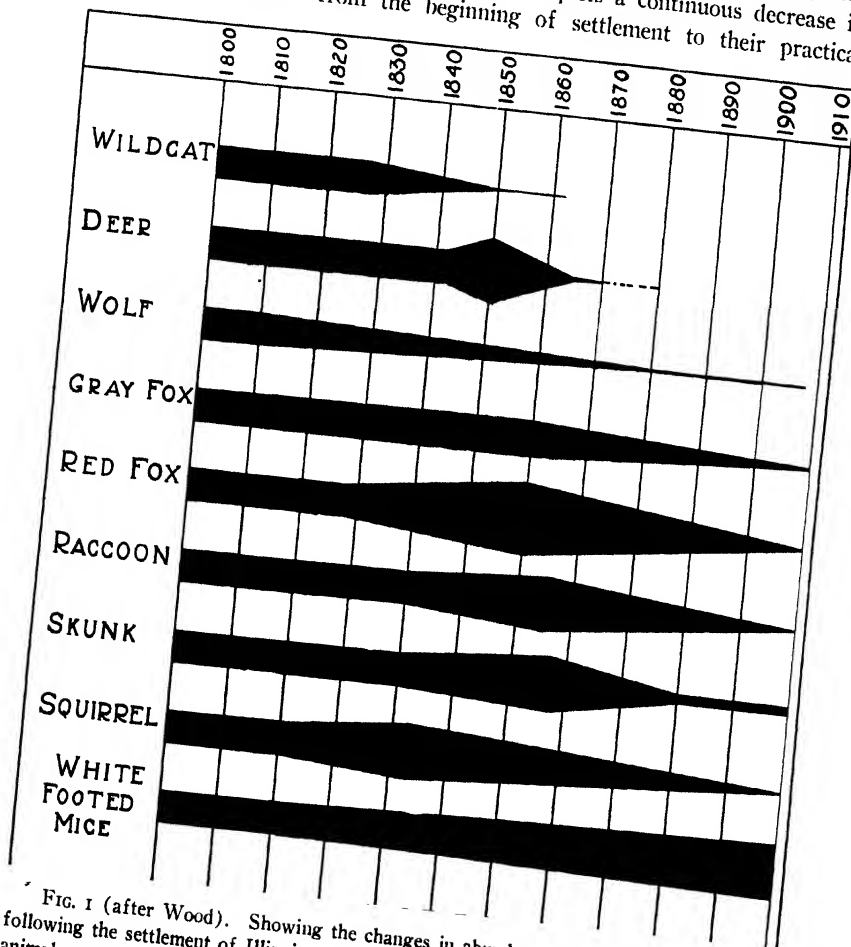


FIG. 1 (after Wood). Showing the changes in abundance of 9 species of mammals following the settlement of Illinois. The wolf, the chief enemy of all kinds of domestic animals, was early sought out and reduced in numbers. The wild cat decreased also. These changes were followed by an increase in the deer and several smaller mammals. The causes of these increases are suggested in figure 3. The natural waves of abundance and scarcity are not indicated, and may have influenced the general estimates.

extinction. When the wolf was reduced to about one half, the deer increased rapidly for a little less than 10 years, reaching a large maximum of about three times the original number. An increase in the raccoon, skunk, squirrel, and red fox began at the same time as the increase in the deer. An examination of the food relations of a number of deciduous forest species (Fig. 2) shows how the decrease in wolves which were large, powerful, and

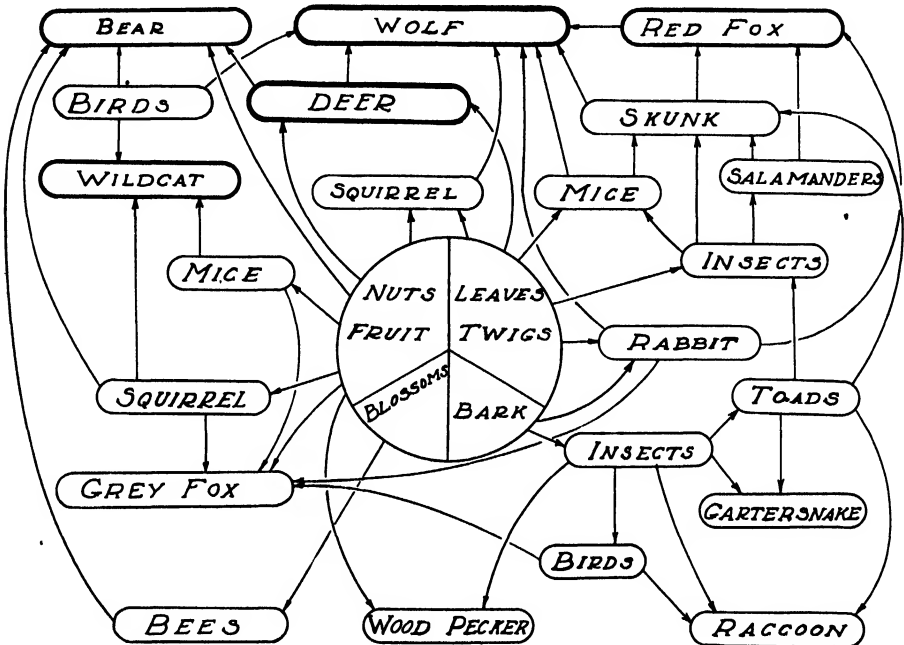


FIG. 2. Showing the food relations of mammals in the deciduous forest as given by Merriam, Korstian, and others. The changes shown in figure 1 are made evident for some of the animals.

numerous, and in wild cats with cunning and especial ability to escape enemies, could permit the marked increase in deer and lesser increases in other animals. It is further noteworthy that an increase in squirrels accompanied the decline in wild cats and wolves. Reference to figure 2 shows this to be clearly possible. The great increase in the deer must have had a considerable effect on herbage, foliage, and on nuts and acorns available for herbivores and omnivores (Korstian, '27). The decrease in food supply of many insects, birds, and mammals, including squirrels and skunks, produced results not here ascertainable. With further decline in deer competitors and wolf and fox predators, a number of mammals increased until the destruction of the forest and persecution by man caused the decline of most of them. These processes indicate what has been usually termed interaction. Some plant ecologists have called the process coaction, of which there are many examples. The Kaibab forest was made a game preserve in 1903.

The destruction of predatory animals, coyotes, mountain lions, etc., was undertaken. The deer is a browsing animal, and has increased in numbers, and reduced the shrubs and small trees of its woodland winter range. This has resulted in the death of many deer from starvation during a recent wave of abundance.

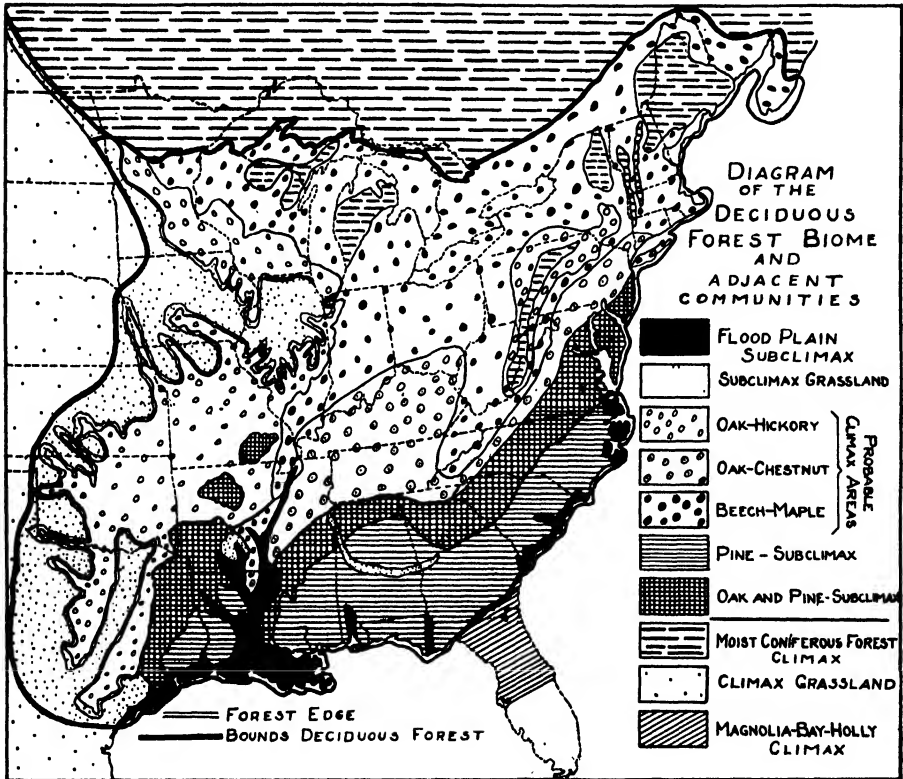


FIG. 3. Showing the deciduous forest biome of eastern North America with its various relations to other communities and its climax and developmental subdivisions. This biome is understood to have been crowded south during the ice age and to have moved back and forth during the various interglacial periods (Adams, '05). Again more recently the grassland is understood to have pushed well into Ohio and again retreated. The forest is generally believed to be invading the grassland.

The subclimax seral areas are indicated by lines, and the diagrammatic limits of the climax areas are indicated with the circles. The mere analogy between the biome and an amoeboid organism is indicated by the greater complexity, which makes the concept applicable only locally for the subclimax parts, which may be likened to the ectoplasm and are different on the several sides. Some of the subclimax parts are large areas. Likewise, the permanent types which might be likened to the endoplasm are of three types and hence again more complicated than the usual conception of an amoeboid organism. The comparison, however, is valuable. The "ingested" portions of the coniferous forest are conspicuous in the diagram, and may have resulted from the northward movement of the biome in recent periods.

2. Subdivisions and Outer Belts in the Biome

It is important to have a clear conception of the various natural divisions of a biome. This is diagrammatically indicated in figure 3 for the deciduous forest. It is evident that the biome differs from the amoeboid organism in having several kinds of "endoplasm." These are the biotic associations. In the deciduous forest, they are: 1. the Beech-Maple-Wood Frog-Plethodon association; 2. the Oak-Hickory-Green Tiger Beetle association; 3. the Oak-Chestnut (not investigated) association (Weaver and Clements, '29). There is a binding network of dominant plants common to the whole area which is a framework or skeleton. Other species of animals and plants fill in this framework.

The seral stages are comparable to ectoplasm. In Illinois where forest

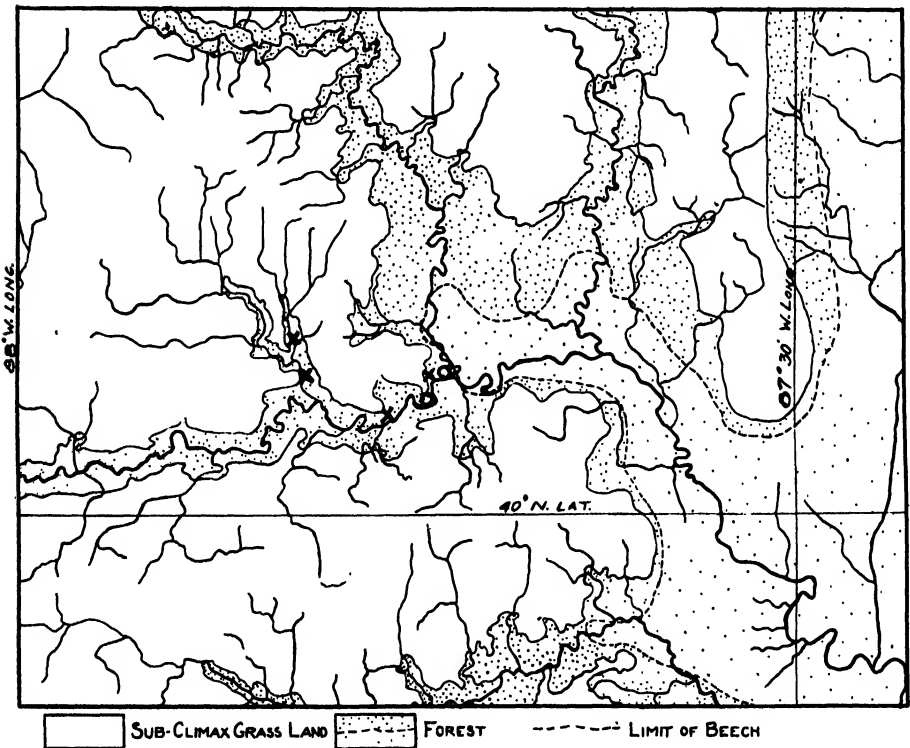


FIG. 4. Showing the advance of the red backed salamander (*Plethodon*) and the snail (*Goniodiscus*) beyond the approximate limits of aggregations of beech trees with which they are commonly associated. The localities are marked thus: o—*Goniodiscus*; x—*Plethodon*.

is moving into prairie (see Vestal, '14 and Gleason, '27), the forest edge is the "ectoplasm" of our imaginary amoeboid organism and must be conceived as comprising several layers. The outermost layer consists of seed-

lings of wild haw and sumac from stones dropped by nesting birds, perhaps in breaks in the grass sod made by moles, pocket gophers or Franklin ground squirrels. The second layer is a narrow band of full grown haws with an intermixture of smaller wild plums supplying the seed to be carried outward by both birds and mammals. The elimination of the sod by the full grown haws permits the invasion by forest trees. Thus the two-layered "ectoplasm" prepares the way for the main body type or endoplasm of the biome. If the climate becomes moister, the outer layer presumably extends more rapidly into the grassland. Birds aid by dropping seeds, and mammals, such as pocket gophers, moles, etc., break the sod and favor the growth of the seeds. If the climate becomes drier the process is reversed. It will be noted (Fig. 4) that there are several kinds of outer layer so that the analogy of the amoeboid organism has to be applied in detail only one one side and a very limited way. On the west, the layers described above as involved in the invasion of grassland are represented by double lines in figure 3.

Invasion such as that of the forest into the prairie is the principal method of migration. In reading treatises on animal distribution one finds instances of pigs swimming the English channel and rodents floating across the Atlantic on logs. The methods of accidental migration are often discussed as though the whole process were incidental and accidental, and as though accident were the chief cause of dispersal. However, in the present geological period it appears that the dominant phenomenon is the invasion of new territory by pioneer organisms which pave the way for others. Following the ice age tundra invaded bare ground; tundra was invaded by coniferous forest; and coniferous forest was invaded by deciduous forest. As an example of the last, the relic of white pine at Oregon, Illinois, is all digested and absorbed except the main skeleton and a little of the filler. The main skeleton is the white pines, and the remaining filler is the few insects which feed on white pine. Most of the herbs, shrubs, and animals belong to the surrounding deciduous forest.

III. THE CONTROL OF INVASION

Physical factors often control invasion. Plants and animals tend to move together as a unit, and are governed by physical factors. Time is required for seeds to reach places made physically suitable for them by other plants. Animals may, because of their motility, find the suitable places in advance of the appearance of the plants. As an illustration of this: 3 or 4 miles west of Danville, Illinois, is the most westerly limit of beech along the 40th parallel of latitude; there are scattered beeches on the upland and numerous trees of this species in the ravines (Fig. 4). Sugar maple is much more common, and extends 100 or more miles farther west. The red backed salamander (*Plethodon cinereus* Gr.) is a common animal associated with the beech. We find it from 2 to 4 miles farther west than the beech in moist

situations where it is to be expected that beech may grow but has not yet gained a foothold due to slower migration. The snail, *Goniodiscus perspectivus* Say, commonly associated with early decay of beech, has been found 2 miles west of the most westerly beech. Its relation to beech has commonly been considered obligate. Again, the green tiger-beetle (*Cicindela sexguttata* Fabr.) has rarely been found by the writer except in oak-hickory forest. This is true in Illinois, Indiana, Tennessee, Massachusetts, and Pennsylvania. Several years of careful observation reveal it only once in red oak-white oak forest without hickory on sand ridges in Illinois and Indiana. Since that observation was made the species has been found with shag-bark hickory seedlings on sand ridges of similar age. There is no relation between this beetle and the particular species of tree; it is predatory.

Sometimes biotic factors may control. The opossum, after 1850, moved northward to Michigan due to cutting timber in the south and killing of wolves, coyotes, and foxes in the north. Michigan is not its natural habitat. It is not as prolific there as in the south, but is holding its own. Animals may control plant migrations, not merely by planting seeds but by other methods. In the western grasslands, with over-grazing, sage brush comes in and holds its own against grasses. When not over-grazed, grass can kill sage brush by taking away water. There is no royal road to generalization.

Wound Healing

Wound-healing is a natural process in constant operation. Streams are depositing new materials on which a community must develop. They are also destroying natural communities by erosion. There is a series of ectoplasmic layers (subclimax stages) constantly taking possession of these areas. Sand areas also show healing "ectoplasmic" subclimax communities. The natural tendency is for the biome to close in and eventually cover all the area with a community suited to the climate. Sometimes this process is exceedingly slow, however.

IV. IMPORTANCE OF DIFFERENT CONTROLS

The questions raised in the preceding paragraph include (1) the relative importance of the various factors believed to control animals and (2) the importance of animals *in* biotic communities, or, *to* plant communities as it might be stated by a plant ecologist.

1. *Law of Tolerance* (Fig. 5)

Factors usually control animals in ways manifested by presence, absence and abundance. Commonly a series of factors or conditions are essential to presence and to any given degree of abundance. The factors must necessarily operate in a manner (Shelford, '12b, '13) suggested by Lebig's

law of minimum for plant growth. According to this law, the growth of an organism is proportional to the nutrient substance present in minimal quantity, no matter how abundant the others may be. Thus food, temperature, light, moisture, etc., may be favorable while shelter is lacking, and an animal which would otherwise be present and abundant, is absent or found in minimal numbers only. The same is true if another condition should vary outside the limits tolerated by the animal. This the writer has called the law of toleration (Shelford, '13, pp. 300-304).

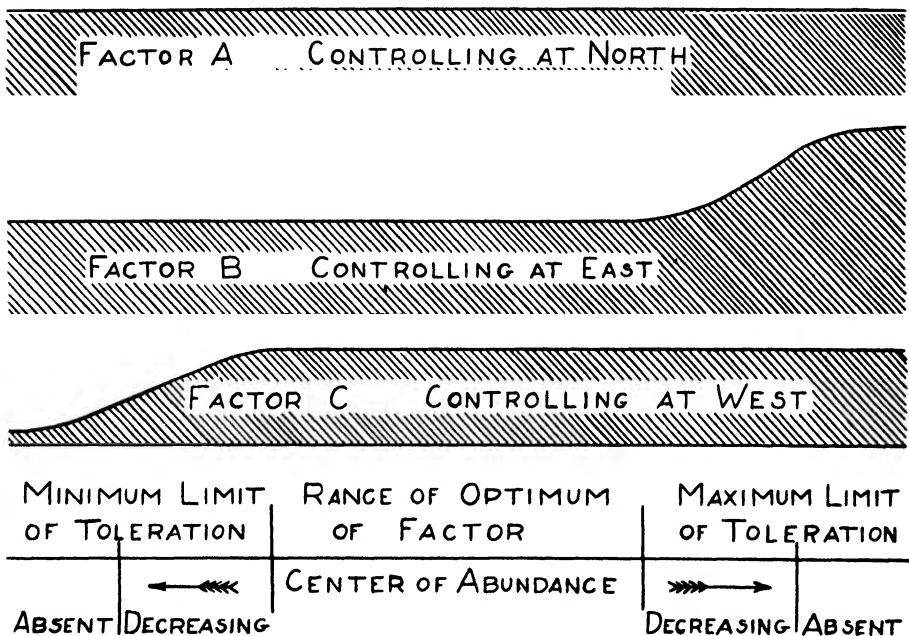


FIG. 5. Illustrating the law of toleration. The abundance of animals is shown below the horizontal line in relation to a group of factors shown above the horizontal line.

2. Food Relations

There is considerable disagreement on the importance given to food by different authors, and frequently much question as to the biotic significance of species whose food habits have been studied. In a comparison of data from a study of the stomach contents of mammals (Merriam, 1884, Körtian, '27), birds (Henderson, '27), reptiles (Surface, '06), amphibians (Kirkland, 1897), fishes (Forbes, 1880, Pearse, '16), and insects (Forbes, 1880, Webster, 1880), especially those called predatory and the phytophagous species covering various localities, dates, and conditions, one is impressed with the fact that each species selects the food available in greatest quantity, making selections which in a particular locality tend to give an erroneous impression as to the specific nature of food relations.

Forbes states (1880, p. 21), "It seems likely to prove to be a general rule that a fish makes scarcely more than a mechanical selection from the articles of food accessible to it, taking almost indifferently whatever edible things the water contains which its habitual range and its peculiar alimentary apparatus enable it to appropriate, and eating of these in about the ratio of their relative abundance and the ease with which they can be appropriated at any time and place."

Animals often choose different food when apparently living under the same physical conditions. Metcalf ('24) showed that various hemiptera follow the physical conditions and feed upon different plants. Some phytophaga which are restricted to particular species occur on the species only under certain physical conditions. He states ('24, p. 174) that "they live in a given habitat because they find there the complex of environmental conditions required and not alone because they find some particular food plants growing there. Some species (*c.g.*, *Pentagramma vittatifrons* Uhler) seem to be more restricted in their distribution than their food plants, whereas other species (*c.g.*, *Megamelanus spartini* Osborn, see Ecology, 1: 195-196) range over a number of food plants provided the plants grow in the region to which they are adapted." The entire question of the food of animals requires re-investigation from the standpoint of plant and animal communities.

V. BIOECOLOGICAL CLIMAXES

As to the importance of animals in biotic communities or to plant communities, the outstanding fact is that the larger mammals were undoubtedly commonly most important and have largely been exterminated in the areas of plant ecological study. The recent work of Bird ('30) in Manitoba showed that even with the considerable changes which have taken place in his locality, the higher vertebrates are of outstanding importance. Generally speaking, the large groups of animals arranged in the order of their importance in land communities are, mammals, birds, insects, lower land vertebrates (chiefly reptiles) lower invertebrates (chiefly arachnids and annelids). From the standpoint of ecology, it is not correct to refer to this as the age of insects, for it is in reality the age of mammals and birds. Referring to man's conquest of nature, it becomes the age of man and insects. These are most important in secondary, especially agricultural, communities.

The often mentioned effect of the bison on grassland is an example, for, if the bison held some of the mixed prairie in a short grass stage, then short grass is the bioecological climax and its proper bioecological designation is *Boutcloua-Bison*, even though the climax with bison excluded is quite different.

VI. DISCUSSION

The large area over which many animals are distributed, and the fact that these areas correspond to largest plant communities, give an animal

ecologist a different viewpoint from that of many plant ecologists, especially the European ones.

In pristine conditions many large and small animals ranged over the largest plant communities, while others were confined to the various sub-communities, and still others were confined to minor variations. All were intimately woven in with the plants and with many interdependencies of cross-pollination, food, soil shifting, etc. There appears to be little room for discussion of abstract concepts of which "pieces are concrete examples." There have never been plant communities without animals or animal communities without plants, and the evidence of the importance of animal influence upon plant communities is growing rapidly (Taylor, '27, Taylor & Loftfield, '24, '25).

How far the partial removal of animals and the destruction of much of the vegetation, leaving only small scattered areas in eastern United States and western Europe, has influenced the philosophy of plant ecologists is difficult to state. The author is, however, confident that many of their difficulties would be lessened if animals were considered.

Animals are better short-period indicators than plants. Their presence and abundance at any hour, day, season, or cycle is indicative of conditions relative to which plants cannot fluctuate at all or must lag behind indefinitely. One thus sees the pushing of the dry-community animals into the wet-community in dry seasons and vice versa as a regular phenomenon (Gleason, '27), with attendant effects upon the habitat.

Another feature of animal community phenomena which is at variance with the numerous academic discussions of succession, is that evidently in many communities composed largely of animals (marine) there is merely development, *i.e.*, forms are added to the pioneer group, with none succeeded by others (Pierron & Huang, '26). This makes it necessary to use "development" in a sense perhaps different from that of Tansley, to cover the growth of communities both where no succession occurs and where succession is an outstanding fact. There are communities where succession is the important and controlling principle; but in others it is obscure or wanting. The dynamics of communities, internal and external, be it seasonal, annual or cyclic, is the clue to their interpretation and to their classification.

SUMMARY

Mammals and birds usually are most important in land communities. Their partial extermination in areas studied by plant ecologists has led to their being ignored. These important animals range over communities of formational rank including their developmental stages. For convenience, the formation is likened to an amoeboid organism with various outer invading layers. In community migrations, animals precede plants in many cases, due to more rapid migration. Factors operate according to limits tolerated

for each factor by the species concerned. The limiting factors differ in different parts of the periphery of the formation, the one which fluctuates beyond the condition tolerated being the limiting factor.

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DISTRIBUTION OF FISHES IN THE BLACK SEA WITH REFERENCE TO BOTTOM CONDITIONS

BASED ON OBSERVATIONS MADE CHIEFLY OFF THE SOUTHERN
COASTS OF CRIMEA

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There is now available a rather large body of observations which permits us to clear up the principal features of distribution of fishes on different bottoms (consequently in different communities), and in this way to explain in general the distribution of fishes on the continental shelf of the Black Sea. The distribution of deposits in the Black Sea, as given by Russian authors, is the following: extensive portions of the Black Sea have depths of over 2,000 meters, and in the central part the depths reach 2,456 meters. Only the narrow strip called the continental shelf, along the coasts, has depths not exceeding 200 meters. This continental shelf or platform is very narrow along the coasts of Crimea, the Caucasus and Turkey, becoming wider only in the western and northwestern parts of the Black Sea. While the width of the shallow part along the southern coasts is 10 miles, it is over 120 miles in the northern part. The whole organic life of the Black Sea is concentrated on this shallow continental platform with depths less than 200 meters. Below this continental platform, on its slopes and in the deeper parts of the Black Sea—which comprise most of it—life is absent (except for bacteria) by reason of presence of hydrogen sulfid. This hydrogen sulfid is oxidized only to depths of 180 meters or, on the continental platform, down to 200 meters. Therefore the thickness of the water layer containing organic life is considerably less in the middle of the Black Sea than along the coasts, where, because of the great mingling of fresh waters and the increased circulation, the water is better aerated and has a lower content of hydrogen sulfid.

The deep basin of the Black Sea is covered, in its western parts with carbonaceous mud, in the central parts with grey clay, and in its eastern parts with a belt of striped mud. The deposits in the deep waters are of no importance in the distribution of living organisms, for the deeper parts of the sea contain nothing living, while the deposits of the continental platform, that is, in the richly populated zone, have a large influence upon the distribution of the life. Along the coasts, in the inner part of the continental platform, are to be found continental deposits (pebble stone, sand, shells, etc.), and farther out there are two zones: first the zone in which the prevailing form is *Mytilus galloprovincialis*, and second the zone with shells of *Modiola phaseolina*. All the deposits are of great importance in the distribution of fishes.

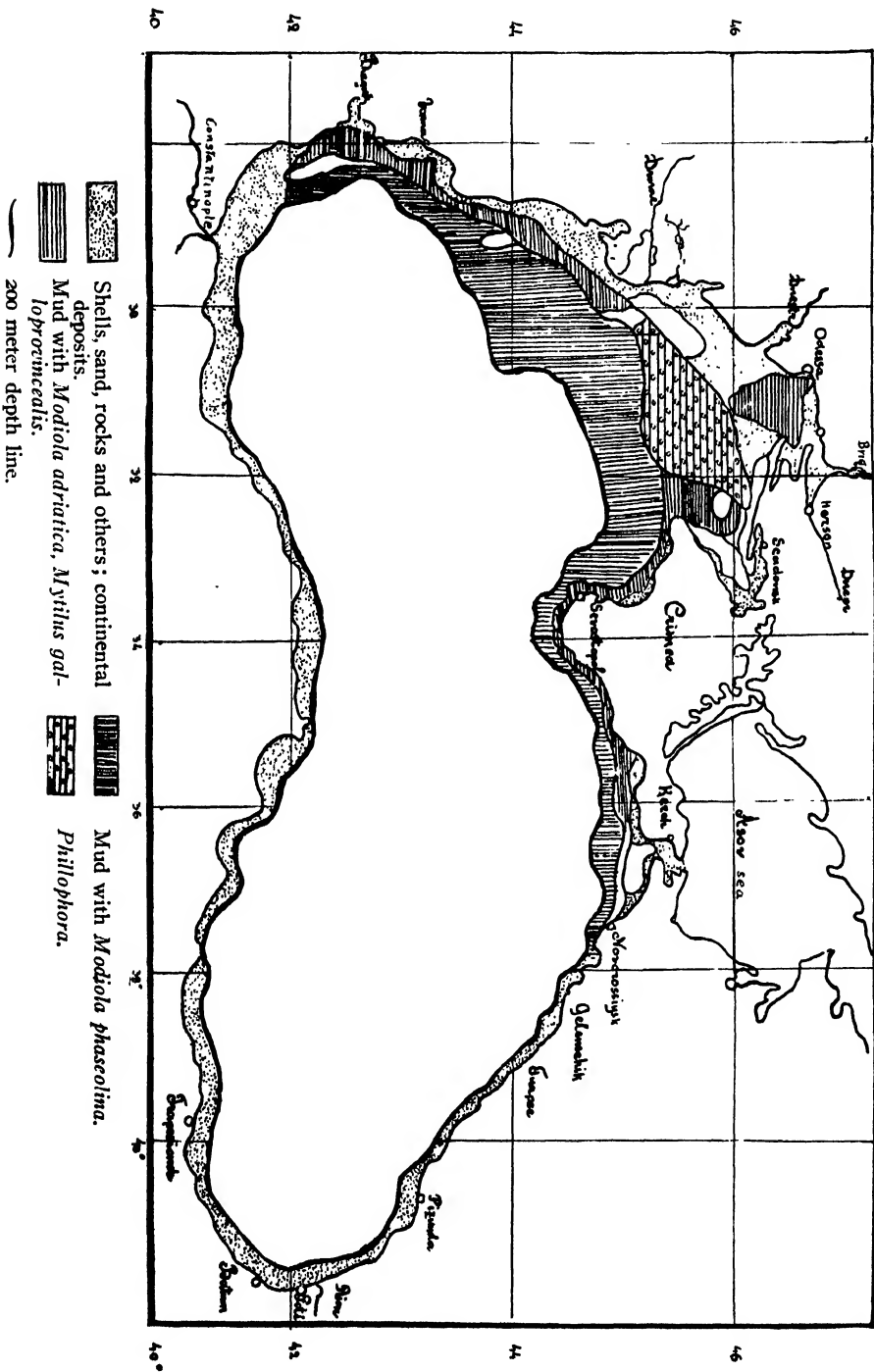


FIG. 1. Map of the Black Sea sediments after Sernov, and others.

The fishes of the Black Sea can be divided into 2 large groups: I, migratory forms, and II, benthic forms.

I. MIGRATORY FISHES

The migratory fishes include such forms as: the Scombridae, Mugilidae, Mullidae, Clupeidae, Engraulidae, Acipenseridae, Pristipomatidae, Sparidae, etc. The life of these fishes is concentrated on the continental platform, and even outside of it in the upper layers of the open sea. As I intend to dedicate a special article to these fishes I shall here touch upon them only briefly. Some forms of migrating fishes prefer a particular deposit, staying there a considerable part of the year, but the larger part of them are to be found in different conditions of the platform.

The migration of all these fishes is greatly influenced by the fact that all of them are migrants from the Mediterranean, and penetrated into the Black Sea in the second postglacial period (about the time of Wurm's glaciation). As they are warm-water forms, they stay mostly near the southern coasts of the Black Sea, but in summer, when the temperature of water over the whole sea becomes equal, and even higher in the northern shallow parts, schools of migrating fishes move from the southern towards the northern parts of the sea. These fishes are, for instance: mullet, herring, anchovy and others, which come to the northwestern portions of the Black and Azov Seas, where they are caught in masses in summer time.

In winter, when the temperature in the Black Sea becomes very low (in the northern parts about 0° C.) and the Azov Sea even freezes in some years, all fishes go to the south, where the temperature is not lower than $6-7^{\circ}$ C. The southern Crimean coast, having in winter almost the same temperature as that of the coasts of Caucasus or Anatolia, is the northern limit at which migratory fishes from the south remain.

It is interesting to note that, owing to particular features of the western and eastern parts of the Black Sea, two races were formed: (1) western, and (2) eastern, each containing such fishes as the anchovy, herring, grey mullets, white sturgeon ("belooga"), etc. A contributing factor is the presence of two circular currents in the Black Sea: one in the western and another in the eastern parts. Both races meet on the Crimean coasts in winter, while in the spring they go in different directions, the western to the region of Odessa, and the eastern to the Azov Sea.

II. BENTHIC FISHES

The benthic fishes of the Black Sea, with limited horizontal migrations, include such forms as: the Blenniidae, Gobiridae, Pleuronectidae, Gobiesocidae, Labridae, Ammodytidae, Syngnatidae, etc. All are shore-fishes, and the character of bottom (consequently of the biocenose) has a great influence upon their distribution.

S. Zernov, who has studied the benthic population along the coasts of Sevastopol, recognized the following biocenoses, connected with the above mentioned deposits of the continental platform.

- I. Biocenose (community) of thickets of *Zostera*.
- II. Biocenose of rocks and flagstones, overgrown by *Cystosira*.
- III. Biocenose of muddy shores.
- IV. Biocenose of sand.
- V. Biocenose of shells.
- VI. Biocenose of mud with *Mytilus*.
- VII. Biocenose of mud with *Modiola phaseolina*.

The distribution of fishes upon these deposits has not been studied enough, and I am trying to do something in that way. The following distribution of deposits can be observed near Sevastopol and along all the Crimea: along the coasts of the open sea there are flagstones and rocks, covered with algae of *Cystosira*, usually reaching depths of 22 meters; beyond the flagstones and rocks there is a strip of sand, descending in the sea to a depth of 35 meters, or of shells sometimes following the sand. This bottom, covered with shells, reaches depths of 60–70 meters, though usually it is at 20–30 meters. In the bays the shells come next to the rocks, at depths of 4–6 meters. Further, in the open sea, the shells or the sand are followed by mud with *Mytilus galloprovincialis*, reaching usually to depths of 28–62 meters (in the bays this mud lies in shallower waters). After the mud with *Mytilus galloprovincialis* there is mud with *Modiola phaseolina*, which covers the continental platform to its very end (from 60–70 meters to 200 meters).

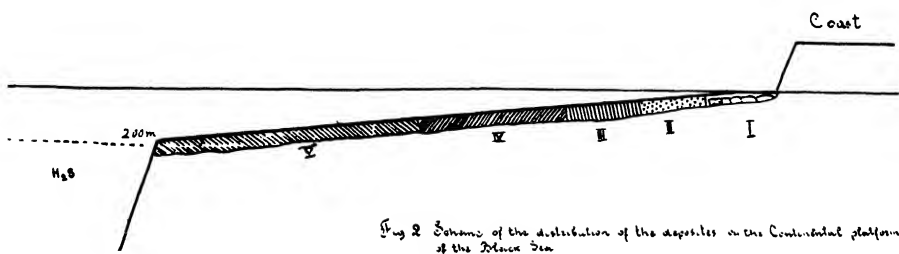


FIG. 2. Scheme of the distribution of the deposits on the Continental platform of the Black Sea. I. Rocks and flagstones overgrown with *Cystosira*. II. Sand. III. Shells. IV. Mud with *Mytilus*. V. Mud with *Modiola phaseolina*.

The distribution of these deposits in the bays is the same as in the open sea, only the width of each strip is narrow; there is also complete absence of the mud with *Modiola phaseolina*. The middle part of the bay is covered with mud containing *Mytilus galloprovincialis*. The coasts are rocky, covered with *Cystosira*. Between the rocky coasts and the mud with *Mytilus galloprovincialis* there are shells or sand. The particularity of these bays is that they have thickets of seaweeds, such as *Zostera nana* and *Z. marina* in

the upper parts, and often in the estuaries of small rivers. The distribution of fishes upon all these biocenoses is very diverse and is characteristic for each kind of deposit. There are, however, always some forms which prevail, while the others are only mingled with them in small numbers. In thickets of *Zostera* there are large numbers of *Crenilabrus ocellatus*, *Cr. cinereus*, *Syphonostoma typhle*, *Zostericola ophiocephalus* and small numbers of other forms. In the thickets of *Cystosira*, on rocks and stone, there occur *Crenilabrus tinca*, *Ctenolabrus rupestris*, *Symphodus rostratus*, *Scorpaena porcus*, *Trigla lucerna* and others. Among the biocenoses of rocks, one finds the shore stones with masses of Blennidae (*Blennius sphinx*, *B. galerita* and others). In the coastal mud near sea-level there are *Poterorhinus marmoratus*, *Gobius melanostomus* and others. In the mud with *Mytilus galloprovincialis* are to be found *Pleuronectes flesus*, *Bothus maeothicus*, *Blennius tentacularis*, *Gobius niger*, *Syngnathus tenuirostris* and others. In the mud with *Modiola phaseolina* are Acipenseridae and others.

It is to be noted that the adult forms are the leading ones for this or that community, while the non adult forms are often met in communities in which the adult forms are not common; for instance: adults of *Serranus scriba* live on flag stones with *Cystosira*, while the non adult forms of this species live in thickets of *Zostera*.

It is curious that each family gives representatives in different communities, that is, very closely related forms sometimes live in quite different communities.

Here are the principal data about the distribution of the fish population:

I. Thickets of *Zostera*

Thickets of *Zostera* occupy all the upper parts of the bays. The fish population is very rich, and the principal leading forms are:

<i>Zostericola ophiocephalus</i>	<i>Nerophis ophidion</i>
<i>Siphonostoma typhle</i>	<i>Crenilabrus griseus</i>
<i>Syngnathus nigrolineatus</i>	<i>Crenilabrus ocellatus</i>

With these are associated: *Mullus barbatus*, *Smaris chryselis*, *Liza aurata*, *Spratella sulinae*, *Sargis anularis*, not belonging to any of the biocenoses. Then there are more rarely forms such as: *Hippocampus hippocampus*, *Crenilabrus tinca*, *Crenilabrus quenquemaclatus*, *Gobius melanostomus*, *Serranus scriba*, *Scorpaena porcus*, *Bothus maeothicus*.

II. Rocks and Flagstones Overgrown with *Cystosira*

Under this biocenose we can consider as a separate biocenose the inshore rocks near the sea-level. Here we can always find:

<i>Blennius sphinx</i>	<i>Blennius gatorugini</i>
<i>Blennius galerita</i>	<i>Tripterygium nasus</i>
<i>Blennius sanguinolentus</i>	<i>Lepadogaster bimaculatus</i>

Rocks and flagstones of deeper waters possess a very rich fish population:

<i>Serranus scriba</i>	<i>Symphodus rostratus</i>
<i>Scorpaena porcus</i>	<i>Corvina nigra</i>
<i>Gobius batrahocephalus</i>	<i>Charax puntazzo</i>
<i>Gobius capito</i>	<i>Chromis chromis</i>
<i>Gobius niger</i>	<i>Proterorhinus marmoratus</i>
<i>Syngnatus acus</i>	<i>Trigla lucerna</i>
<i>Syngnatus tenuirostris</i>	<i>Lepadogaster bimaculatus</i>
<i>Crenilabrus tinca</i>	<i>Lepadogaster gouani</i>
<i>Crenilabrus quenquemaclatus</i>	<i>Lepadogaster decandolii</i>

and many others.

III. Sand

Coarse sand containing broken shells is populated by amphipods and their usual companion *Ammodytus cicerellus*. The compact sand is populated by numerous species of fishes such as:

<i>Ophidium barbatum</i>	<i>Solea nasuta</i>
<i>Trachinus draco</i>	<i>Callionymus festivus</i>
<i>Uranoscopus scaber</i>	<i>Callionymus belenus</i>

Typical inhabitants of sand bury themselves in it and only some forms remain on its surface.

IV. Muddy Shores

Muddy shores are to be found in the upper parts of bays. In these places, near the very surface of the water, we find:

<i>Proterorhinus marmoratus</i>	<i>Gobius melanostomus</i>
and, somewhat deeper:	
<i>Syngnatus nigrolineatus</i>	<i>Pleuronectes flesus luscus</i>
and others.	

V. The Biocenose of Shells

Shells are also rather richly populated. The following forms can be considered as characteristic for this biocenose:

<i>Lepadogaster bimaculatus</i>	<i>Blennius tentacularis</i>
<i>Syngnathus acus</i>	<i>Gobius niger</i>
<i>Syngnathus tenuirostris</i>	<i>Pomatoschistus minutus</i>

and others.

VI. The Biocenose of Mud with *Mytilus galloprovincialis*

The mud with *Mytilus* is especially populated with:

<i>Gobius niger</i>	<i>Bothus maeothicus</i>
<i>Syngnathus tenuirostris</i>	<i>Pleuronectes flesus luscus</i>
<i>Blennius tentacularis</i>	<i>Raja clavata</i>

and others.

TABLE I. The distribution of the principal (mostly typical) species of fish of the Crimean coasts in different communities

+ = frequent, in great quantity; × = rare, in small quantity; — = absent

Fishes	Zostera	Muddy shores	Cystosira		Sand	Shells	Mud	
			Coastal stones	Flag stones and deep drawing stones			with <i>Mytilus galloprovincialis</i>	with <i>Modiola phaseolina</i>
1. <i>Raja clavata</i> L.....	×	—	—	—	×	×	+	+
2. <i>Huso huso</i> (L.)	—	—	—	—	—	—	—	—
3. <i>Acipenser stellatus</i> Pall.....	—	—	—	+	—	—	+	+
4. <i>Anguilla anguilla</i> (L.)	×	+	—	—	—	—	—	—
5. <i>Atherina pontica</i> Eichw.....	×	×	×	×	—	—	—	—
6. <i>Mugil cephalus</i> L.....	×	×	×	×	×	—	—	—
7. <i>Ammodytes cicerellus</i> Raf.....	×	×	—	—	×	—	—	—
8. <i>Mullus barbatus ponticus</i>	×	×	×	×	+	×	—	—
9. <i>Serranus scriba</i> L.....	×	—	—	+	—	—	—	—
10. <i>Charax puntazzo</i> L.....	×	×	×	×	—	—	—	—
11. <i>Sargus anularis</i> L.....	×	×	×	×	×	×	—	—
12. <i>Smaris chryselis</i> Cuv. et Val.....	×	×	×	×	×	×	—	—
13. <i>Chromis chromis</i> L.....	—	—	×	×	—	—	—	—
14. <i>Labrus prasostictes</i> Pall.....	—	—	—	+	—	—	—	—
15. <i>Crenilabrus rostratus</i> Bl.....	×	—	×	+	—	—	—	—
16. <i>Crenilabrus quinquemaculatus</i> Bl.....	×	—	×	+	—	—	—	—
17. <i>Crenilabrus linca</i> L.....	—	—	—	—	—	—	—	—
18. <i>Crenilabrus ocellatus</i> Forsk.....	+	—	×	×	—	—	—	—
19. <i>Crenilabrus cinereus</i> Lac.....	+	—	×	×	—	—	—	—
20. <i>Ctenolabrus rupestris</i> L.....	×	—	×	+	—	—	—	—
21. <i>Scorpaena porcus</i> L.....	—	—	×	+	—	+	—	—
22. <i>Trigla lucerna</i> L.....	—	—	×	+	—	—	—	—
23. <i>Latrunculus pellucidus</i> (Nardo).....	×	+	×	×	—	—	—	—
24. <i>Gobius melanostomus</i> Pall.....	×	+	×	—	—	—	—	—
25. <i>Gobius batrahocephalus</i> Pall.....	×	—	×	+	—	—	—	—
26. <i>Gobius capito</i> L.....	—	—	×	+	—	—	—	—
27. <i>Gobius niger</i> L.....	—	—	—	—	—	+	+	—
28. <i>Proterorhinus marmoratus</i> Pall.....	×	+	×	—	—	—	—	—
29. <i>Pomatoschistus minutus</i> Pall.....	—	—	—	+	—	+	—	—
30. <i>Zostericola ophiocephalus</i> Pall.....	+	—	—	—	—	—	—	—
31. <i>Callionymus festivus</i> Pall.....	—	—	—	—	+	—	—	—
32. <i>Trachinus draco</i> L.....	—	—	—	×	+	—	—	—
33. <i>Uranoscopus scaber</i> L.....	—	—	—	×	+	×	—	—
34. <i>Lepadogaster bimaculatus</i> Pen.....	—	—	+	×	+	+	—	—
35. <i>Lepadogaster gouani</i> Lac.....	—	—	×	×	—	—	—	—
36. <i>Tripterygium nasus</i> Risso.....	—	—	—	—	—	—	—	—
37. <i>Blennius galerita</i> L.....	—	—	+	+	—	—	—	—
38. <i>Blennius tentacularis</i> Br.....	—	—	×	×	—	+	+	—
39. <i>Blennius sanguinolentus</i> Pall.....	—	—	+	×	—	—	—	—
40. <i>Blennius pavo</i> Pall.....	—	—	+	+	—	—	—	—
41. <i>Blennius sphinx</i> Cuv.....	—	—	+	×	—	—	—	—
42. <i>Ophidium barbatum</i> L.....	—	—	—	—	+	—	—	—
43. <i>Pleuronectes flesus luscus</i> Pall.....	×	×	—	—	×	×	+	—
44. <i>Bothus maeothicus</i> Pall.....	—	—	—	×	×	×	×	—
45. <i>Arnoglossus kessleri</i> Schm.....	—	—	—	×	×	×	×	—
46. <i>Solea nasuta</i> Pall.....	—	—	—	—	+	×	×	—
47. <i>Lophius piscatorius</i> L.....	—	—	—	—	—	×	×	—
48. <i>Gadus euxinus</i> Nordm.....	—	—	—	—	×	×	×	—
49. <i>Motella tricirrata</i> Bl.....	×	—	×	+	×	×	×	×
50. <i>Hippocampus hippocampus</i> L.....	×	—	—	+	×	×	—	—
51. <i>Syphonostoma typhle</i> L.....	+	×	×	×	—	—	—	—
52. <i>Syngnathus acus</i> L.....	—	—	—	×	—	×	×	—
53. <i>Syngnathus tenuirostris</i> Rathke.....	—	—	—	×	—	+	+	—
54. <i>Syngnathus nigrolineatus</i> Eichw.....	+	+	—	×	—	×	—	—
55. <i>Nerophis ophidion</i> L.....	+	×	×	×	—	×	—	—
56. <i>Syngnathus schmidtii</i> Popov.....	—	—	—	—	+	×	×	×

Gobius euxinus, *Syngnathus Schmidti* and others are usual forms for the region of mud characterized by *Mytilus*.

VII. *Mud with Modiola phaseolina*

This community is much poorer than the preceding one. Here we have for the most part: *Bothus macothicus*, *Raja clavata*, *Squalus acanthias*, *Gobius euxinus* (in water), etc.

The short review of biocenoses shows that typical forms occur mostly in the biocenose of rocks and flagstones as well as in the biocenose of *Zostera*. In the course of the year considerable vertical migrations of separate components of the biocenoses are observed. Thus, in winter it seems that the dogfish goes deeper in the region of flagstones. Many forms also leave *Zostera* for flagstones, etc.

SUMMARY

The fish of the Black Sea live upon the continental platform, which extends to a depth of 200 meters. The deep waters are lifeless because of the hydrogen sulfid which they contain.

Two main divisions of the fish are recognized, (1) migratory, (2) benthic. The former winter on the southern shore, and migrate to the northern coast in summer.

The benthic forms are divided into biocenoses related to the type of bottom. Five types of bottom are distinguished: (1) rocks and flagstones overgrown with *Cystosira*; (2) sand; (3) shells; (4) mud with *Mytilus*; (5) mud with *Modiola phaseolina*. There are also the *Zostera* thickets, the muddy shores and two divisions of the *Cystosira* rocks and flagstones, making 8 communities. The principal species of each of the 8 communities are given.

INFLUENCE OF FOREST LITTER ON THE GERMINATION AND EARLY SURVIVAL OF CHESTNUT OAK, *QUERCUS* *MONTANA*, WILLD.

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INTRODUCTION

In studying the factors which affect the germination and early survival of oaks, Korstian ('27) has pointed out that moisture, temperature and compactness of the surface soil are of the utmost importance. Biotic factors, especially those causing destruction of the acorn or of various parts of the seedling, must also be considered in the natural regeneration of oak forests. The effect of forest litter in modifying these factors to conditions favorable for germination and early survival have been pointed out by several investigators. In recent publications both Korstian ('27) and MacKinney ('29) have shown that a covering of forest litter exerts a modifying effect on soil temperature at the ground surface and insures the most favorable temperature conditions for acorn storage that can be secured under natural conditions.

During the autumn of 1928 an exceptionally heavy crop of chestnut oak acorns was observed in Ohio and Indiana. The stand of seedlings which appeared the following spring presented an unusual opportunity for a study, under actual field conditions, of the important factors affecting the germination and early survival of chestnut oak. It seemed reasonable to expect that the findings of such a study, although limited to a single species, would also have some bearing upon the germination and early survival of the other oaks, for which opportunities of study were lacking.

Robert B. Gordon, Department of Botany, Ohio State University, and the author obtained in the late spring and early summer of 1929, data from 60 half-milacre (.0005 acre) quadrats in Ashland, Fairfield, Hocking and Scioto counties, Ohio. On these quadrats all seedlings were counted, and, in addition, height measurements were taken on a random sample amounting to at least 20 per cent of the total number of seedlings on the quadrats. After several depth measurements, the leaf litter was removed from each quadrat, and the acorns which had not produced seedlings were gathered and classified according to the apparent cause of their failure. Data such as the kind and amount of other vegetation present, soil, overhead shade, slope,

¹ The work was done while the author was attached to the Central States Forest Experiment Station.

aspect, etc., were also recorded for each quadrat. Of all the factors studied which might possibly have affected germination and early survival, analysis of the data showed that litter depth, aspect, and to a certain extent overhead shade, were the only factors which could be definitely correlated with germination and early survival. With the exception of nut weevils, biotic factors which are of paramount importance in some regions were comparatively unimportant in areas covered by the present study. Korstian and others have pointed out that acorn-eating animals may be responsible for the almost complete destruction of an acorn crop. However, no indications of such complete destruction, even locally, were noted during the present study. Deer, bear and turkeys, which are known to be heavy consumers of acorns, are negligible factors in Ohio. Although present, squirrels could not be considered numerous; and the presence of other desirable mast in the forest tended to reduce their inroads on the acorns of chestnut oak.

WEATHER CONDITIONS

Climatological data from Lancaster and Portsmouth, Ohio, the stations nearest the two main regions covered, were analyzed. This was done to determine what weather conditions prevailed during the period of acorn germination and the early establishment of the seedling stand.

As chestnut oak belongs to the white oak group, the acorns germinated soon after falling in the autumn of 1928. During August, September and October of 1928 the precipitation at both Portsmouth and Lancaster was considerably below the mean monthly rainfall for those stations. During November it became about normal and remained well within the normal range of precipitation during the winter months. At Portsmouth, precipitation during March and April, 1929, was only slightly below average, but during the important growth period in May it was 2.5 inches above the mean. Very little rain fell during March at Lancaster, but during April and May considerably more than an average rainfall occurred. At both stations June was dry, the precipitation being over 1.5 inches less than the monthly mean at both places.

With the exception of September, mean monthly temperatures for the period August–December, 1928, were above the average for both localities. For the period January–June, 1929, mean monthly temperatures were below average in both localities, except for March and April when warmer weather than usual prevailed.

The above facts are of significance in their relation to the environmental factors surrounding the acorns. For instance, during the dry fall months of 1928 when the acorns began germination, the retention of moisture by leaf litter was of the utmost importance. During the following April and May, when precipitation was approximately normal or considerably above, these same environmental factors assumed a relatively smaller degree of

importance. The moisture conserving properties of forest litter have been pointed out by Groves ('14) who found a greater amount of moisture in the surface soil of the forest than in adjacent cultivated fields, and attributes this fact to the humus layer in the woods. Zon ('27) has partially summarized investigations of this type all of which show the ability of the forest litter and humus to conserve moisture.

IMPORTANCE OF FOREST LITTER

The term "loose litter" as used here may be defined as the uncompacted layer of leaves immediately above the past year's fall of acorns. In general,

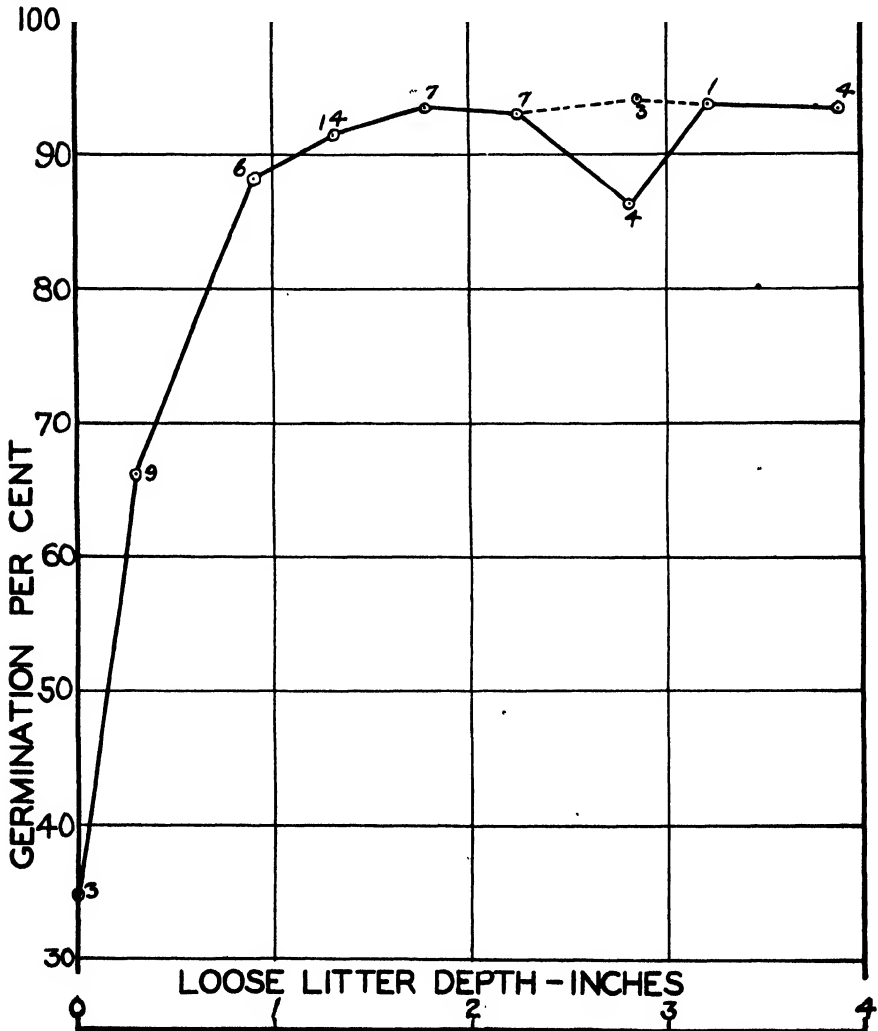


FIG. 1. Relation of germination per cent to loose litter depth. Broken line shows trend of data with elimination of one quadrat which occupied an unusually exposed situation.

it consists of the past season's fall of leaves and has not yet visibly begun to disintegrate. Below the loose litter, and furnishing the bed upon which the acorns rest, is a layer of leaves grading from compacted leaves in the initial stages of decay to totally decomposed material at or near the surface of the mineral soil. This latter layer has been called "compact litter and humus."

In figure 1 is presented the average germination per cent for the quadrats in each half inch loose litter depth class. The germination per cent for a single litter depth class was computed by adding all sprouted acorns from all quadrats in a class and computing its percentage of the total number of acorns which fell on all quadrats in the class. The number of quadrats in each litter depth class accompany the plotted points on the graph.

Figure 1 indicates clearly that much higher germination occurred on those quadrats with a loose litter depth of approximately one inch and over than on quadrats with a scantier covering of leaves. A further trend is also indicated in that there is relatively little significant change in the germination per cent with increase in litter depth above one inch. The broken line in figure 1 indicates the trend of the data after the elimination of one quadrat from the average of the class. This quadrat had a germination of only 60 per cent, and examination of the physical description showed that it differed from the rest in that it had a minimum of overhead shade and occupied a very exposed position on a southeasterly slope.

Although the depth of loose litter beyond a certain point had little effect upon total germination per cent, the effect of litter depth upon the development of seedlings was much more significant. The plotted points in figure 2 show that the highest production of green seedlings occurred on quadrats falling within two litter depth classes, namely, 0.6-1.0 and 1.1-1.5 inches. In this group of quadrats the minimum litter depth was 0.7 inches and the maximum 1.5 inches. This indicates that a leaf covering of approximately .75 to 1.5 inches offers the most desirable conditions for the early establishment of chestnut oak seedlings. Figure 2 further indicates that a shallower covering results in a much lower per cent of green seedlings, and that a steady decrease also occurs with increasing depth beyond approximately 1.5 inches.

As might be expected, this decrease in plant per cent with increasing litter depth is accompanied by an increasing percentage of etiolated seedlings.

Subsequent observations of permanent quadrats have shown that seedlings present in an etiolated condition under the leaf litter, at the time the leaves of the majority of the seedlings are fully formed, have little or no ability to come through the litter and establish themselves. Reexamination of permanent quadrats upon which the protective leaf litter covering had been removed showed also that even under a dense overhead shade, etiolated seedlings thus exposed seldom complete their development, but apparently wither and die within 3 or 4 weeks.

Undoubtedly the dry weather prevailing through June had considerable

bearing upon the mortality of both protected and exposed etiolated seedlings. Depth of leaf covering also has a marked effect on the stem length of seedlings, the relation being roughly an inch of height added for each additional inch of covering. Heights were measured from the tip of the living shoot to the point of attachment of the stem with the acorn. Although seedling stems grown in the deepest litter were taller, this greater height alone is not necessarily desirable. In most cases these taller seedlings had weak, thin and crooked stems, and could not be preferred to the shorter, more stocky

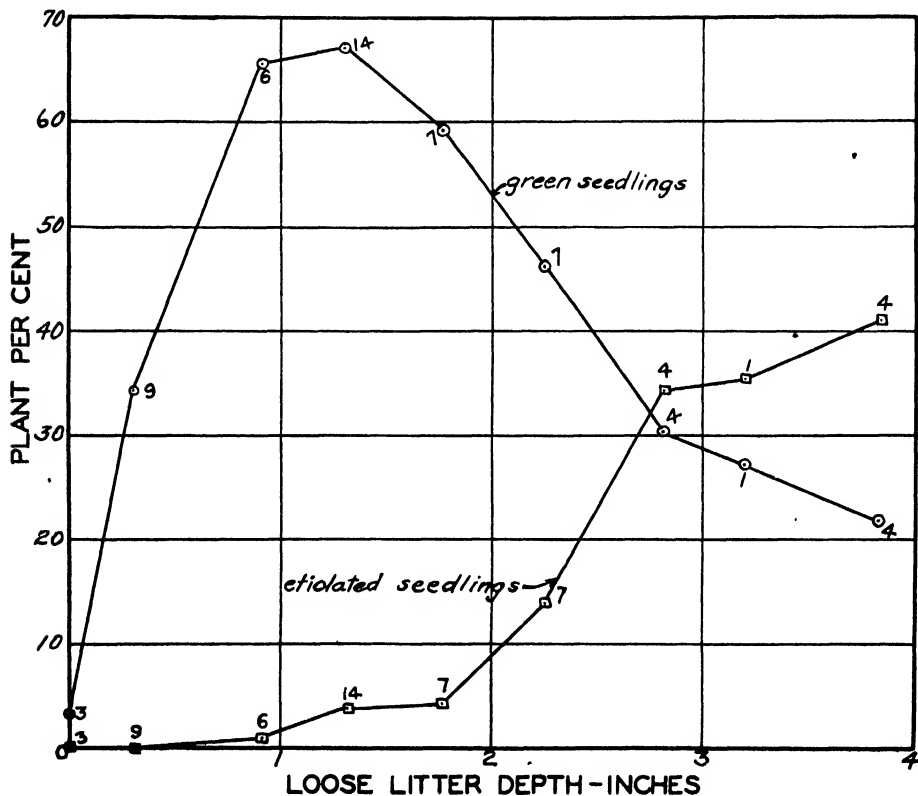


FIG. 2. Graphic presentation of the effect of leaf covering upon the percentage of acorns producing green and etiolated seedlings.

The combined percentages of green and etiolated seedlings in this figure do not equal the total percentages of germination shown in figure 1 because part of those which germinated were killed by insects and other agencies (see Table I).

stemmed type. Permanent quadrats established between June 14 and 30, 1929, were reexamined in the latter part of July. Comparison of seedling height measurements made at the time the quadrats were established and again at the reexamination showed that no increase in height had taken place on any quadrat, indicating that the first season's height growth had been completed at least by the middle of June.

A further analysis was made to determine the possible effect of density of stocking on height growth and plant per cent. The number of seedlings per quadrat varied from 4 to 443. Even when quadrat data were grouped, with other variables fairly constant, no correlation between stocking and height growth or plant per cent could be discovered. This only substantiated the generally recognized fact that during much of its early life the oak seedling draws its nourishment from the acorn, and that the first season's growth is



FIG. 3. The dense stand of chestnut oak seedlings has developed under conditions well suited to its germination and early survival. Forest Service photograph 237327.

largely independent of competition between the trees of the seedling stand itself.

It is interesting to translate the stand figures from quadrat to an acre basis and note the tremendous ability of this species to reproduce. The minimum stocking is at the rate of 8,000 seedlings per acre while the maximum reaches a total of 886,000 per acre. Nor was the latter figure unusual since an effort was made to establish quadrats where density of stocking was average for a given set of conditions. Figure 3 illustrates the completeness with which such a seedling stand covers the ground.

EFFECT OF ASPECT AND OVERHEAD SHADE

That aspect may have a considerable effect upon germination has been slightly considered in the discussion of total germination per cent. As shown in figure 1, loose litter depths of 0.9 inch and over had an approximately constant effect upon germination per cent. For the study of possible relationships between aspect and germination, all quadrats with litter depths under 0.9 inch were sorted out and the remaining quadrats were grouped by aspects and by the various degrees of overhead shade in each aspect. Average figures show that the overhead shade on quadrats of northerly and southerly aspects was approximately the same. The average germination, however, was found to be 93.8 per cent on northerly aspects as against 79.9 per cent for southerly facing quadrats. Only one quadrat was obtained on a west aspect, but those that faced due east had a somewhat greater degree of overhead shade and an average germination of 94 per cent.

The data for each aspect showed that a small but significant increase in germination per cent took place with an increase in overhead shade. A separate analysis for those quadrats having less than a 0.9 inch litter cover showed little or not correlation between germination per cent and the factors of aspect and overhead shade. The lack of sufficient litter cover reduced the germination per cent to such an extent that any effect of the other factors was obscured.

EFFECT OF BIOTIC FACTORS

As the acorns which had not produced seedlings were removed from each quadrat they were classified according to the apparent cause of failure. Acorn counts were omitted on some quadrats because later observations were to be made and it was desirable to leave the leaf litter undisturbed.

Table I presents the results from acorn counts of 55 quadrats.

TABLE I. *Condition of acorns which did not produce seedlings*

Based on examination of 5,772 acorns occurring on 55 quadrats.

Condition of acorns	Number of Quadrats on which condition was found	Average of all acorns which fell on all quadrats per-cent
Sprouted acorns, dead, damaged by insects	55	20.99
Not sprouted, damaged by insects	55	14.30
Sprouted but dead, due to drought, freezing and undetermined causes	27	1.37
Seedlings dead, root rot	34	1.27
Roots present, but shoots absent, probably bitten off	28	0.97
Acorns sprouted dead, damaged by animals, mostly roots bitten off	9	0.52
Acorns not sprouted, embryos dark, hard or mouldy.		
No insect or animal damage	19	0.37
Normal embryos, unsprouted	2	0.03

From Table I it is obvious that the most common destructive agency affecting acorns was insects. Nut weevils were by far the most prevalent but a small amount of damage by gall insects also was noted.

Although nut weevils and gall insects were apparently the greatest single cause of failure, their presence in an otherwise sound acorn did not always result in failure to germinate or in death shortly after germination.

The acorns attached to 400 well developed seedlings were examined during the course of the field work. Only 240 of these were found to be free from the attacks of either nut weevils or gall insects. Larvae or emergence holes of the weevil were found in 150 acorns, the remaining 10 being attacked by gall insects only. The latter were probably present in many acorns also attacked by the nut weevil, but, due to the work of the latter insect, the evidence of their presence was unrecognizable. In spite of the rather high percentage of failures due to nut weevils and gall insects, it is apparent that a fair percentage of chestnut oak acorns so infested can still produce healthy seedlings. Damage to acorns or seedlings as listed in the last six conditions in Table I present in the aggregate a very small percentage of the total number of acorns. However, some of the more outstanding observations made in connection with this classification deserve comment. It was impossible in the present study to determine the agency causing destruction of the young shoots. In practically all cases classified under this condition, the shoot had been removed very close to the point of its junction with the acorn. The presence of a callus was the only clue as to whether the shoot had been bitten off or whether the plumule had not yet developed. A separate classification of such seedlings was necessary since it was not possible to determine whether the removal of the shoot was due to biting insects or small rodents.

The most common type of animal damage was found in deep litter where small burrowing animals bit the roots an inch or two below the acorn. This was apparently done when the seedling roots became an obstruction in the burrow.²

SUMMARY

1. Maintenance of a good forest litter is essential for the successful germination of chestnut oak, and best results are obtained where the leaf covering is 1 inch and over in depth.

2. Early survival of chestnut oak is also dependent upon loose litter, best results occurring where the covering is from 1 to 2 inches in depth. Above and below these depths the percentage of seedlings which become established is greatly reduced.

² In the autumn of 1929, while working on a chestnut oak seedling project on the Clark County State Forest, Indiana, Benjamin Lucas, Field Assistant, Central States Forest Experiment Station, reported that he had observed a species of long-tailed wood mouse cutting the roots of seedlings and eating them.

3. Germination per cent on southerly slopes is lower than on north or east slopes, due probably to the relatively longer period of exposure to sunlight and consequent greater evaporation.
4. On any one aspect, where the loose litter covering is 1 inch or greater in depth, a small but significant increase in germination per cent takes place with increase in density of overhead shade.
5. In southern Ohio the most important biotic factor adversely affecting the acorn crop was nut weevils.
6. The presence of nut weevil larvae in a chestnut oak acorn may not always result in failure, a fair percentage of well developed seedlings being produced from acorns so infested. This may be due to the large size of chestnut oak acorns, the cotyledons being able to withstand a certain amount of weevil damage and still furnish nutriment for the development of seedlings.

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OBSERVATIONS ON THE AMMONIA CONTENT OF SEA WATER

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I

It has recently been suggested by H. Wattenberg¹ that it is advisable to pay more attention to the ammonia dissolved in the sea water as a source of nitrogen for the vegetable plankton, and to determine it as a nutrient of the same value as phosphate and nitrate. That this has been relatively seldom done has been due chiefly to the lack of a suitable method for the estimation of NH_3 in the very diluted condition in which it is present in sea water.

A suitable method for the estimation of NH_3 in sea water which avoids distillation of the sample and also avoids, by the use of suitable reagents, the precipitation of the alkaline earths by the alkaline Nessler's reagent, has been described by Wattenberg¹ and is here given in essential detail.

A 100 cubic centimeter sample of sea water is treated with 5 cc. of 30 per cent solution of rochelle salt, and this mixture is then added slowly to a 10 cc. solution of 20 per cent sodium hydroxide. Then 2 cc. of Nessler's reagent (prepared according to Treadwell) are added, and, after 15 to 45 minutes, the color developed is compared with the color of a standard solution of NH_3 treated in the same way.

Standard solutions of NH_3 are prepared in the following way: sea water of the same salinity as the water to be analyzed is made slightly alkaline and then diluted with distilled water to 1.5 times its volume. The whole is then boiled down to the original volume, and the resulting turbidity is cleared up by the addition of as little HCl (NH_3 free) as possible. The water is then stored by stopping the mouth of the bottle with a U-tube filled with pumice stone and sulphuric acid. Standard NH_3 solutions are made up to suitable concentration for comparison with the samples under examination.

Because of the very small quantities of ammonia present in sea water, the reagents must be carefully freed of ammonia and then stored in bottles stoppered as above described. The sodium hydroxide solution was diluted with 50 per cent of its volume of distilled water and boiled down to the original quantity, and the rochelle salt solution, after being made slightly alkaline with NaOH , was treated in the same manner. Using the purest chemicals obtainable and treating the reagents in this manner, it was never

¹ Wattenberg, H. A simple method for the direct estimation of ammonia in sea water by the use of Nessler's reagent. *Rapp. et Proces-Verbaux*, Vol. LIII, Mars 1929

possible, under the working conditions of the seaside laboratory, to reduce the blank value much below 15 mgm. N per cubic meter.

For the comparison of colors, both 30 cm. Nessler tubes and a Duboscq colorimeter were used. Each type of apparatus has its advantages and disadvantages. With each series of determinations it is necessary that a blank value be determined in order that correction may be made in the final result for NH_3 present in the reagents.

II

A number of observations on the ammonia content of the waters of Frenchmans and Penobscot Bays were made by the author while at the Mt. Desert Island Biological Laboratory during the months of August and September 1930. The results so far obtained must be regarded as preliminary, and, while showing great variation, they indicate the magnitude to which nutrient substance is present in the sea water of the area investigated.

Surface values of ammonia nitrogen in Frenchmans Bay ranged from 0 to 48 mgm. per cubic meter. The largest quantity, 187 mgm. N per M^3 , was recorded from a depth of 10 meters at the head of the Bay. Invariably the ammonia content increased from surface to bottom of the water column. A typical example of the distribution at two separate stations is indicated by curves *A* and *D* in figure 1.

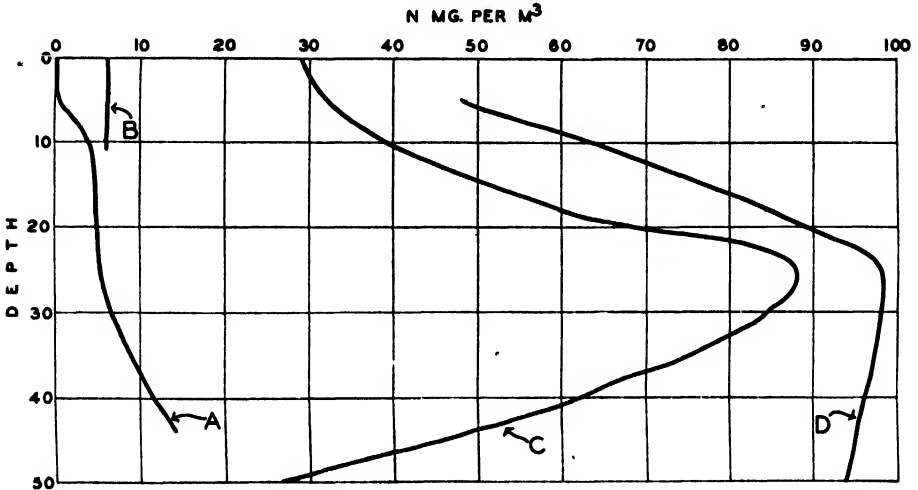


FIG. 1. Vertical distribution of ammonia nitrogen for Frenchmans Bay, stations 8 (curve A) and 10 (curve D), and for Penobscot Bay, stations 21 (curve C) and 23 (curve B), August 1930. Horizontal scale of curve C is one fourth of actual value.

Ammonia observations were made at two localities in Penobscot Bay. At station 21, near the mouth of the Bay, very much greater amounts of ammonia were found than at station 23, in the Penobscot River. At the former station (curve C) the ammonia nitrogen ranged from 116 mgm. per

cubic meter at the surface to 350 mgm. at 25 meters; while at the latter station (curve B) on an ebbing tide the column of water, 11 meters deep, contained uniformly 6 mgm. per cubic meter, and on the rising tide 6 hours later 9 mgm. of ammonia nitrogen were recorded for the surface and less than 1 mgm. for the subsurface water.

III

Preliminary to an investigation of the bottom deposits as sources of nutrient material, a number of bottom mud samples were collected from near the laboratory dock and allowed to stand with measured amounts of sea water for given periods of time. In all cases it was found that after the sample of water had stood for several hours with the bottom deposit the ammonia nitrogen content was increased. The following experiment is typical of the results obtained.

Three samples of sandy mud were collected from a depth of three meters near the laboratory dock and put into pyrex flasks with 200 cc. of sea water collected at the same time and containing less than 1 mgm. per cubic meter of ammonia nitrogen. The flasks were shaken thoroughly and at the end of fifteen hours the water was filtered through several thicknesses of filter paper until clear, and the ammonia determined. The following results were obtained:

Sample	Weight of Mud after Drying	Gain of N in Mgm. M ¹ in 15 Hour Period
1	27.4 gms.	7
2	65.3 gms.	9
3	70.0 gms.	9
Blank	—	0

In every case the ammonia content of the water increased in varying amounts on standing with the bottom deposit. The type of bottom deposit must necessarily enter into account in a quantitative investigation, for it is quite possible that different types of deposit would contain and yield to the sea water different amounts of NH_3 .

While the work on the ammonia content of sea water this past summer was only preliminary, the observations do give an idea of the magnitude of the results to be expected. The observations on the amount of NH_3 taken up by sea water on standing with bottom deposits opens up the possibility that the sea bottom of bays and inlets may be one of the important sources of nutrient materials, particularly so in areas of strong vertical circulation.

SUMMARY

In connection with studies of the nutrient salt content of sea water, observations on the ammonia nitrogen content of the water in the vicinity of Mt. Desert Island, Maine, were made during the summer of 1930.

Ammonia nitrogen was determined by adding Nessler's reagent to fresh samples of sea water previously treated with salt seignette and sodium hydroxide. The yellow brown color developed was compared to that developed by sea water of standard ammonia nitrogen content treated in the same way.

The results obtained show great variability, as is the case with other nutrient salts in this region. Ammonia nitrogen in the surface water of Frenchmans Bay ranged from 0 to 48 mgm. per cubic meter. The largest quantity observed was 350 mgm. per cubic meter from a depth of 25 meters in Penobscot Bay.

A preliminary investigation of the ammonia nitrogen content of the bottom sediments suggests the possibility that they may be important sources of nutrient salts for Frenchmans Bay.

ECOLOGICAL RELATIONSHIP OF THE GENUS *POMATIOPSIS*
WITH SPECIAL REFERENCE TO *POMATIOPSIS*
*LAPIDARIA*¹

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In a recent paper in *ECOLOGY*, Professor B. Shimek ('30a, p. 681) makes the following comment on the little snail, *Pomatiopsis lapidaria*. "It should be recorded again that the operculate snail *Pomatiopsis lapidaria*, which is still being reported as a freshwater form, is strictly terrestrial." In the same number of *ECOLOGY* (p. 788) the writer called attention to the amphibious nature of this species; and Professor Shimek, in a reply to the writer's notes, reaffirms its strictly terrestrial nature. In another place (Shimek, '30c, p. 38) the statement is made that "Mr. Baker again persists in calling *Pomatiopsis lapidaria* an amphibious species, thus contradicting himself, for in his 'Fresh Water Mollusca of Wisconsin' (1928) he says of this species: 'Though essentially a terrestrial animal, the gill is of the usual pectinated form as found in the Amnicolidae. Few specimens have been personally collected in water but it has been found in many places under leaves and on damp or wet mud in places more or less subject to overflow from streams and rivers.'" It is to be noted that Professor Shimek, in quoting this statement, has fallen into the too common error of repeating *only* the part that affects his own view of the matter, for the preceding sentence of the reference quoted reads: "*Pomatiopsis lapidaria* is distinctly an amphibious snail, although seemingly in many localities to prefer wet ground to actual immersion in water" (Baker, '28, p. 166).

Writing of this species in the Mollusca of the Chicago Area (Baker, '02) the writer says: "Living in fresh water or on land (amphibious), frequenting, when in water, the vicinity of fresh-water plants; when on land preferring moist localities." The writer has contended for thirty years that this species is amphibious and has never deviated from this belief.

Reference to the literature reveals the fact that few authors have given much attention to the ecology of the species, often copying the opinions of others. In his original description of the species Say (1817, p. 13) says of the species, *Cyclostoma lapidaria*: "Found under stones, etc., in moist situations, on the margins of rivers. Like those of the genera *Lymnaea* and *Planorbis* this animal possesses the faculty of crawling on the surface of the water, in a reversed position, the shell downward." Stimpson and Lewis

¹ Contribution from the Museum of Natural History, University of Illinois, No. 63.

(1865, p. 30), while admitting the amphibious nature of the species, refer to its habits as those of a land mollusk. However, on page 4 of Stimpson's paper, the group Pomatiopsinae is referred to as amphibious. Pilsbry (1896, p. 37) states that "The best-known species *P. lapidaria* is as much a terrestrial mollusk as most of the Succineas. They cannot live for any length of time immersed in water, and I have drowned specimens, just as land snails may be drowned, by confining them in a vessel full of water. Information upon the other species is less definite, but *P. cincinnaticensis* at least seems to be of aquatic habits." *Pomatiopsis hinkleyi*, described in the same paper, lives in the original habitat on a steep rocky bank in moss and decaying vegetation kept constantly wet by spray from the falls (Hinkley's description of habitat). *Pomatiopsis lapidaria* has the same kind of habitat, living on rocks wet by the spray from Niagara Falls (Letson, '01, p. 242).

ECOLOGICAL STATION OF *POMATIOPSIS LAPIDARIA* IN ILLINOIS

This species has been found in 4 localities in Champaign County, Illinois, in more or less abundance. The habitat relationships of the species in these places are as follows:

Collections Made by Professor Frank Smith and the Writer

Flood plain of Sangamon River, three-fourths of a mile below Mahomet, in a small, cool stream about 2 feet wide and 6 inches deep, the bottom composed of mud and fine sand. The banks bordering this stream are low, and, in the spring, are covered with water to the depth of a few inches. Specimens were collected in July, 1918, when the surrounding flats were dry and the only water in the vicinity was the small stream fed from a spring in the glacial bank of the Sangamon River. *P. lapidaria* was abundant in the stream and was found *only* in this situation although it could easily escape from it, the banks in several places being so sloping that progression up them would not be difficult. Then, too, this species is able to float foot upward on the under surface of the water film and could thus reach land. Associates of *Pomatiopsis* in this stream were *Fossaria parva* (Say) and *Fossaria modicella* (Say), the *Fossaria* living both in the water and on the wet mud bordering the stream, especially where it emptied into the Sangamon River. A description of this habitat has been published (Baker, '22, p. 60).

Collections Made by Professor Frank Smith, H. J. Van Cleave and the Writer

Flood plain of Salt Fork of the Vermilion River, at Homer Park, in small stream about 2 to 3 feet wide and from a few inches to a foot in depth, the bottom of mud with some sand (Fig. 1). Specimens were collected both in the stream and on the wet mud bordering the stream. In this place

more individuals were found on the wet mud than in the water of the stream. Collections in this habitat have been made at all times of the year, and no specimens have been observed in dry situations, although they have been found under wet leaves on low ground. The greater part of this region becomes filled with asters, golden rod, and other summer and fall flowers following the wet season of spring.



FIG. 1. Flood plain of Salt Fork River at Homer Park, near Homer, Illinois. Site of small brook at base of bank in background, flowing into Salt Fork. Picture taken in May during flood period. *Pomatiopsis lapidaria* living in water near base of trees as well as in brook.

Collections made by Professor H. J. Van Cleave and the Writer

Flood plain of Salt Fork, a quarter of a mile east of previous locality. The margin of the river is covered with old logs and tree debris piled up by

former floods (Fig. 2). *Pomatiopsis* was found in water 6 inches deep at the margin of the river, associated with *Physa gyrina*.

Terrestrial associates on the flood plain of the river are *Polygyra fraterna* (Say), *Zonitoides arborea* (Say), *Haplotrema concavum* (Say), *Retinella hammonis* (Strom.), and *Pseudovitrea minuscula* (Binney). No *Succinea* has been found associated with *Pomatiopsis* in the localities listed.



FIG. 2. Flood plain of Salt Fork River, a quarter of a mile below Homer Park, river to right of picture. *Pomatiopsis lapidaria* living in water near shore associated with *Physa gyrina hildrethiana*. Picture taken in May during flood conditions.

Professor H. J. Van Cleave has collected Mollusca extensively in the vicinity of Urbana, and his statement of the finding of *Pomatiopsis lapidaria* follows: "There are two localities in the immediate vicinity of Urbana where *Pomatiopsis* has been found in relative abundance. One of these is a small stream emptying into the Salt Fork River at Homer Park, near Homer, Illinois, and the other is a small stream just northeast of the Big Four shops in Urbana. In the latter, before it became ruined as a collecting spot by conversion of its banks to a public dumping ground, *Pomatiopsis* was observed for a number of years. This locality was visited with a class of graduate students in Zoology chiefly for observation of the undisturbed forms of life in the stream. Almost invariably, *Pomatiopsis* was crawling over the dead leaves in the bottom of the stream. A small *Physa* (*P. gyrina hildrethiana*), *Pisidium concinnulum*, and *Fossaria modicella* were the chief associates in this habitat."

THE *POMATIOPSIS* OF THE PLEISTOCENE

In the loess and other Pleistocene geological deposits in Iowa, Illinois, and other states, there occur in greater or less number fossil *Pomatiopsis* related to *lapidaria*. Professor Shimek contends that these are wholly land species because associated mostly with species known to be wholly of terrestrial habits. Professor Shimek states that the fossil *Pomatiopsis* are rare in the Iowa loess deposits, but are more common in some other states. The writer's statement that the little fresh water snail *Fossaria parva tazewelliana* always occurs with *Pomatiopsis* in loess deposits is disputed as being quite inaccurate, Professor Shimek stating that only 2 out of 22 exposures contained the *Fossaria*, and that only 7 specimens were found in these deposits.

Examining the material from Illinois deposits of true loess, so identified by Dr. M. M. Leighton, Chief of the Illinois State Geological Survey, an authority on Pleistocene geology, it is found that *Pomatiopsis* is found in 10 exposures out of 59, and that *Fossaria* occurs with 8 of these, in number from 4 to more than 50. But the *Fossaria* occurs in 22 exposures, or in 12 without *Pomatiopsis*, and the latter occurs in only 2 exposures without *Fossaria*. This shows that in the loess alone *Fossaria* occurs in about 38 per cent of the exposures. In 109 exposures of all kinds containing land species *Fossaria* occurs in 42, or in 39 per cent.

In 44 exposures of Peorian loess in the museum collection, *Pomatiopsis* occurs in 6, always associated with *Fossaria*. The number of *Pomatiopsis* in the six exposures were 1, 3, 3, 3, 26, 1. The number of *Fossaria* found in 22 exposures of Peorian loess were as follows: 2, 5, 6, 5, 2, 52, 18, 40, 13, 3, 1, 4, 4, 11, 6, 4, 53, 68, 5, 1, 1, 7. In a deposit of silt containing land species there are 67 *Pomatiopsis* and 42 *Fossaria*. The total number of *Fossaria* in loess deposits of Peorian age is 311 specimens, far more abundant than *Pomatiopsis* which numbers but 37 specimens. In Yarmouth loess deposits, *Pomatiopsis* occurs in 6 out of 15 and *Fossaria* in 7 out of 15, the two species being associated in 4 deposits. These figures appear to indicate that the writer was correct in stating that *Fossaria* occurs in a large percentage of loess formations associated with *Pomatiopsis*.

As the terrestrial character of the exposures in which these two species occur may be questioned, a list of species found in several Peorian loess deposits is given below.

Fulton County, 3.5 miles east, 1.75 miles south of Lewistown. *Polygyra monodon*, *Polygyra multilineata wanlessi*, *Haplotrema concavum*, *Retinella hammonis*, *Euconulus fulvus*, *Columella alticola*, *Vertigo loessensis*, *Gonyodistus anthonyi*, *Gonyodiscus macclintocki*, *Vallonia gracilicosta*, *Succinea ovalis pleistocenica*, *Succinea grosvenori gelida*, *Hendersonia occulta*, *Carychium exile canadense*, *Fossaria parva tazewelliana* (18 specimens).

Fulton County, 3 miles south, 1.5 miles west of Lewistown. *Retinella hammonis* *Polygyra multilineata wanlessi*, *Columella alticola*, *Vertigo loes-*

sensis, *Gonyodiscus anthonyi*, *Goniodiscus macclintocki*, *Helicodiscus parallelus*, *Succinea grosvenori gelida*, *Succinea retusa fultonensis*, *Pomatiopsis scalaris* (26 specimens), *Fossaria parva tazewelliana* (68 specimens), *Stagnicola caperata* (2 specimens).

The above material was collected by Dr. Harold Wanless, of the Department of Geology, University of Illinois, under the direction of Dr. Leighton. There are more than 20 exposures of this nature from Fulton County in the material collected by Dr. Wanless. About a dozen deposits from Indiana, Kentucky and Ohio include *Fossaria* and *Pomatiopsis* in 4, although in only one were the two species associated.

The little *Fossaria parva* and *modicella* are quite as averse to immersion in water as are some of the Succineas, repeatedly crawling out of a dish when in the laboratory. They are more often found on wet mud by the margin of a stream than actually in the water, although they do live in the water at one time or another. They are truly amphibious, and the association of the little fresh water pulmonates with *Pomatiopsis* is not, therefore, surprising.

The Specific Relationship of the Fossil Pomatiopsis

The distinctness of the Pleistocene form of *Pomatiopsis* from the recent *lapidaria* has been questioned. Several years ago (Baker, '27, p. 119) the writer separated the fossil *Pomatiopsis* from the recent species under the name *Pomatiopsis scalaris*, the type locality being the loess at New Harmony, Indiana. A careful study of 150 specimens of the recent *lapidaria* in distribution from Illinois east to New Jersey and from Michigan south to Alabama, in comparison with 182 specimens of the fossil form, mainly from loess deposits of Illinois, Indiana, and Kentucky, shows the following differences, which are very uniform: the fossil form is narrower, the whorls rounder and the sutures deeper; there are usually $7\frac{1}{2}$ whorls (6-7 in *lapidaria*), the seventh whorl being much wider and resting on the sixth whorl turban-like (in *lapidaria* this whorl usually shows only as a small knob-like elevation); the body whorl is of less height, measuring 1.85 mm. in *scalaris* and 2.1 mm. in *lapidaria*; the umbilicus is uniformly larger in *scalaris*; the aperture is rounded and not as much elongated as in *lapidaria*, and the upper part is rounded. These differences are quite as great as those between *lapidaria* and *hinkleyi* and the fossil form should be separated specifically from *lapidaria*.

Regarding distribution in time, *scalaris* occurs in Yarmouth, Sangamon, Peorian, and Early Wisconsin deposits. I do not find it recorded from Aftonian deposits, but I do not doubt its presence in this interval.

In Illinois, *scalaris* disappears in Early Wisconsin deposits, in which, also, true *lapidaria* appears, and all *Pomatiopsis* of this form examined from Late Wisconsin deposits in Illinois are referable to the form with narrow umbilicus, high whorls, and more angulated aperture. Outside Illinois, how-

ever, true *lapidaria* occurs associated with *Fossaria parva* in deposits of apparently Sangamon age in the forest bed and associated strata near Lawrenceburg, Indiana, this age being assigned by Leverett ('02, p. 367). The specimens examined are not from the deposits on the Ohio River but in the valley of the Miami River, and the complexity of the deposits at this locality suggests that Sangamon and later strata may be represented in the section studied. The *lapidaria* form occurs in deposits believed to be of Yarmouth age from the bank of the White River, in Arkansas County, Arkansas, associated exclusively with a large fluviatile fauna. The *Pomatiopsis* of the loess of Crowley's Ridge in eastern Arkansas is *scalaris* and not *lapidaria*. In the Niagara gravels, supposed to be of Late Wisconsin age, the *Pomatiopsis* appears to be *scalaris* rather than *lapidaria*, judged by the few specimens examined.

Recently (Baker, '30, p. 424) the statement was made concerning *Pomatiopsis scalaris* that it "is obviously related to *lapidaria* and is without doubt the ancestor of that species." Since that observation was made collections have been examined from Arkansas and Indiana in which true *lapidaria* occurs in strata of Yarmouth and Sangamon age. It is apparent, therefore, that two species are represented in Pleistocene time, *scalaris*, found largely in loess and old soil horizons, and *lapidaria* in aquatic and some land deposits, the two forms occupying the same territory, but perhaps differing in ecological habits. Both of these species will be figured in a paper on Pleistocene species of Mollusca now in press.

It is to be noted that these geological decisions are based on a very large collection of Pleistocene molluscan life, over 45,000 specimens carefully named and with duly authenticated stratigraphic data by competent geologists being in the Natural History Museum of the University of Illinois. More than 600 different exposures are represented from the states of Iowa, Illinois, Indiana, Arkansas, Missouri, Kentucky, Ohio, Michigan, Wisconsin, New York, New Jersey, and Canada.

SUMMARY

Pomatiopsis lapidaria is not wholly and exclusively a land mollusk as maintained by some conchologists, but is truly an amphibious species, living immersed in water at different times and in different places. In the same habitat it may be found in water in the spring and under leaves or in wet places in summer and fall. That it voluntarily lives in water at times is shown by its presence in small brooks when it was possible to escape to a drier situation on land. It is not amphibious in the sense that *Succinea retusa* is, but in the sense that the small lymnaeids of the *Fossaria* group are. The associates of *Pomatiopsis lapidaria* in Illinois and Indiana are *Fossaria parva*, *Fossaria modicella*, and *Physa gyrina hildrethiana*, the *Physa* occurring in two localities. *Pisidium concinnulum* occurred in one brook habitat.

The Pleistocene species of *Pomatiopsis* is usually associated with the

little fresh water pulmonate *Fossaria parva tazewelliana* in deposits of undoubted loess. The *Fossaria* has been found to be more abundant in loess deposits than the *Pomatiopsis*, occurring in 38 per cent of the exposures of loess containing fossils. In 109 exposures containing land species *Fossaria* occurred in 42, or 39 per cent, and was represented by from 1 to 68 specimens in the collections examined. The number of *Pomatiopsis* in the loess collections varied from 1 to 26.

The *Pomatiopsis* group of the loess, from Yarmouth to Early Wisconsin time, is separable from the recent *lapidaria*, the umbilicus being wider, the body whorl narrower and of less height, the aperture rounder, and the apical whorl larger and wider. The name *scalaris* should be used for the fossil species answering to this diagnosis, which occurs most abundantly in loess deposits. *Lapidaria* also occurs throughout the Pleistocene, from Yarmouth to the present time, in both aquatic and land deposits. It is evident that these two species lived contemporaneously throughout Pleistocene time, but that *lapidaria* is the only one to come down to the recent period, *scalaris* disappearing largely during Early Wisconsin time, but a few possibly surviving until Late Wisconsin time.

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CORRELATION BETWEEN PLANT COMMUNITIES AND THE REACTION AND MICRO-FLORA OF THE SOIL IN SOUTH CENTRAL TEXAS

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The occurrence of vegetation areas differing significantly from the general vegetation area in which they are found, and from each other, thereby making climatic factors appear not critical, prompted an investigation of the soil factors in certain of these areas. According to Clements ('20), every plant is a measure of the conditions under which it grows, and every habitat is a complex in which the factors are almost inextricably interwoven. The first factors to receive attention were soil reaction and micro-flora. These, and other soil factors, together with their interrelationships, are under further investigation. The present account has to do with the soil reaction, the numbers and distribution of micro-floral groups, and the occurrence of higher plant communities.

SOILS INVESTIGATED

Soil studies were made in Bastrop, Gonzales, Bexar, and Travis counties in south central Texas. Bastrop and Gonzales counties belong to the Gulf Coastal Plain and to the later Eocene of the Cenozoic. The two counties are included by Tharp ('26) in the same vegetation area, which he calls Alternate Zones of Oak-Hickory and Blackland Prairie. The particular regions under observation are a forest of mixed pine and hardwood in Bastrop county near the town of Bastrop, and a marsh in the valley of the San Marcos river in Gonzales county near the village of Ottine. These regions were selected because, in a limited area, the plant cover is strikingly different from that of the surrounding country, both areas being far to the west of regions in which the respective plant cover is typical. Since they differ only edaphically from adjacent regions, these areas thus offer a unique opportunity for soil studies.

The main portion of the pine in Bastrop county is confined to the Mt. Selman geological formation, which is characterized by red sandy clay overlain with gravel and flint pebbles, and underlain with a blue clay. At its eastern limits certain clayey sands come in which are of Cook Mountain age (Dufval). The western limit of the pine sharply marks the exposed contact of the Carrizo and Mt. Selman formations. The Carrizo is a series of light colored sands and sandy clays, and supports a growth of oak-hickory with mesquite-chaparral in localized areas. The dominant vegetation of the pine "island," which is 80 miles west of other pine in the state, consists of loblolly

or oldfield pine (*Pinus taeda*),¹ post oak (*Quercus stellata*), and blackjack oak (*Q. marylandica*), with sand oak (*Q. cinerea*) at its northern edge, and cedar (*Sabina sabinoides*) at the west. Soils for study were selected in growths of oak, pine, pine-oak, pine-cedar, oak-cedar, sedge-myrtle from a marshy area in the pine-oak, and of oak-hickory, and mesquite-chaparral. The characteristic plants in each of the foregoing are given below, after Table I.

Lying as a sinuous strip, about 2 miles long and 600–1,000 feet wide in the flood plain of the San Marcos river, the Gonzales marsh is fed by seepage from the adjacent sand hills. Ottine is near the line of contact between the Mt. Selman and Cook Mountain formations. The soil of the marsh appears not to belong to either of these formations, but is river alluvium or river terrace material, or both, deeply burying the underlying rock. The edges of the marsh in all probability represent Mt. Selman material (Deussen, '23). The vegetation includes many eastern species unknown this far west, differing sharply from the post oak-blackjack of the surrounding country and the usual river bottom vegetation known to this section of the state. Post oak and blackjack associated with elm (*Ulmus crassifolia*) and hackberry (*Celtis mississippiensis* and *C. reticulata*) are found on the slope leading down to the marsh. Where the sandstone hills make contact with the marsh proper fragmentary sphagnum beds occur, the soil being chiefly peat to which sand has been added from the slope as wash material. Water ash (*Fraxinus lanceolata*) associated with burr oak (*Q. macrocarpa*), red oak (*Q. rubra*), Shumard's oak (*Q. shumardii*), black walnut (*Juglans niger*), hollies (*Ilex vomitoria* and *I. decidua*), occasional poplars (*P. deltoides*) and willows (*Salix nigra*), and sabal palms (*Sabal glabra*) mark the abrupt transition to real marsh conditions, the soil being a dark colored gummy silt. The area is periodically flooded, being wettest in early spring. The series of flats extending to the river bed include a sedge meadow, where one of the dominants is myrtle (*Morella cerifera*), this species being the same as that found on marsh soil in Bastrop county. The soil of the sedge-myrtle is a sandy silt of high organic content, being of the quaking bog type, having a more or less constant water level. Soil studies were made in the oak-elm-hackberry slope, and in the sphagnum, ash, and sedge-myrtle associates.

The studies in Bexar and Travis counties were made in order to compare soils of similar plant communities. Mesquite-chaparral from the Midway-Wilcox hills, oak-hickory from the Carrizo, and oak-cedar from the Glenrose geological formation were selected in Bexar county, and oak-cedar on Austin chalk and Edwards limestone, in Travis county.

METHODS

Soil samples for each soil studied were collected at three places 10–15 feet apart at depths of 4 and 12 inches, those for bacteriological determina-

¹ Plant names are according to Lewis, '15, Sargent, '22, and Small, '13.

RESULTS

TABLE I. Soil reaction and micro-flora in south central Texas, at 4 and 12 inch depths.

The columns after pH under each county give the micro-flora. The total number is the total of all microorganisms per c.c. of air dry soil, the number in the column to be multiplied by 10⁶. The figures under the columns A, F, and B represent percentages of actinomycetes, fungi, and bacteria, respectively, of the total.

[illegible]

tions being taken under sterile conditions. A trench was dug 12–30 inches long and 12–20 inches wide, and the soil taken from the side at the desired depths. Composite samples were obtained for each depth by thoroughly mixing the three. The pH value of the soil extract was determined by the colorimetric method, an adaptation of the Gillespie method being used (Committee on Bacteriological Technic of the Society of American Bacteriologists, '26), and checked electrometrically. The soil extract was prepared according to Wherry ('26b).

Soil dilutions were made to 1/500,000, the higher dilutions being used for plating. From 3 to 9 plates were made for each dilution used. Where it is necessary not only to count the total number of colonies but to differentiate between the colonies on the plate, it was found practicable to use the dilutions that would give 10–20 colonies on a plate 100 millimeters in diameter. Soil extract agar and Brown's albumin agar (Smith and Worden, '25, Waksman, '16, '19, Waksman and Fred, '22, Jones and Murdock, '19, Brown and Halversen, '19, Werkenthin, '15, and Williams, '25) were compared on the first samples in order to ascertain which would give the maximum total count and still not permit the overgrowth of molds. Egg albumin agar gave the most satisfactory and constant results. Frequent checks with soil extract and beef extract agars gave approximately the same total counts as those obtained on the albumin agar, although neither was satisfactory for long incubation periods due to overgrowth and drying. Plates were incubated at room temperature. Bacteria developed in 3–5 days; fungi in 3–7 days; actinomycetes in 8–15 days. The counting was done by inspection, with a binocular and compound microscope when necessary for identification. Computations were made per gram of air dry soil.

Table I shows the soil reaction and the micro-flora at 4 and 12 inches, respectively, for the different plant associations. The values in the table represent, not single determinations for a given association in a given county, but values compiled from the data obtained for different areas in the same association at the same and at different seasons of the year, and in some cases from observations extending over a period of several years.

Figures 1, 2, and 3 are graphic presentations of the results shown in Table I, being made by averaging the results for similar associations irrespective of county.

The oaks in Bastrop oak (Table I), oak-hickory, oak-cedar, and pine-oak are *Quercus stellata* Wang. and *Q. marylandica* Muench. The same oaks are found in the Bexar oak-hickory, and in the Gonzales oak-elm-hackberry. *Q. cinerea* Michx. is associated with these species in the pure oak in Bastrop county. *Q. virginiana* Mill. is the species in the oak-cedar associations in Bexar and Travis counties. The pine in all of the associations is *Pinus taeda* L.; hickory, *Carya buckleyi* Durand; mesquite, *Prosopis glandulosa* Torr.; elm, *Ulmus crassifolia* Nutt.; hackberry, *Celtis mississippiensis* Spach. and *C. reticulata* Torr.; cedar, *Sabina sabinoides* Small; and the chaparral

species include one or more of the following, *Adelia pubescens* Kuntze, *Berberis trifoliolata* Moric., *Condalia obovata* Hook., *Colubrina texensis* A. Gray, *Zizyphus obtusifolia* A. Gray, and *Opuntia lindheimeri* Engelm.

The Bastrop sedge-myrtle associes contains *Morella cerifera* Small, *Eleocharis acicularis* R. & S., *E. arenicola* Torr., *Panicum condensum* Nash, *P. lindheimeri* Nash, *Juncus diffussimus* Buckl., *J. bufonius* L., and *Pteridium aquilinum* Kuhn; the Gonzales sedge-myrtle, *Morella cerifera*, *Eleocharis tortilis* Schultz., *E. arenicola*, *E. tenuis* Schrad., *Panicum anceps* Michx., *P. condensum*, *P. jorii* Vasey, *Juncus effusus* L., *Andropogon glomeratus* B. S. P., *Erianthus compactus* Nash, *Typha latifolia* L., *Sagittaria falcata* Pursch, and *Pteridium aquilinum*. The Gonzales ash associes includes *Fraxinus lanceolata* Borek., *Ilex vomitoria* Ait., *I. decidua* Walt., *Hicoria pecan* Brit., *Ulmus crassifolia*, *Quercus shumardii* Buckl., *Q. macrocarpa* Michx., and *Sabal glabra* Sarg. The sphagnum associes includes sphagnum, higher mosses, ferns, liverworts, duckweeds, water cress, iris, orchids, and other hydrophytes.

DISCUSSION

Figure 1 shows the relation of plant associations to the pH of composite soil samples to 12 inches. While it is true that the first 6 inches of a soil are significant in the establishment of a seedling and in the succeeding competition, the lower strata are important, and particularly significant, both

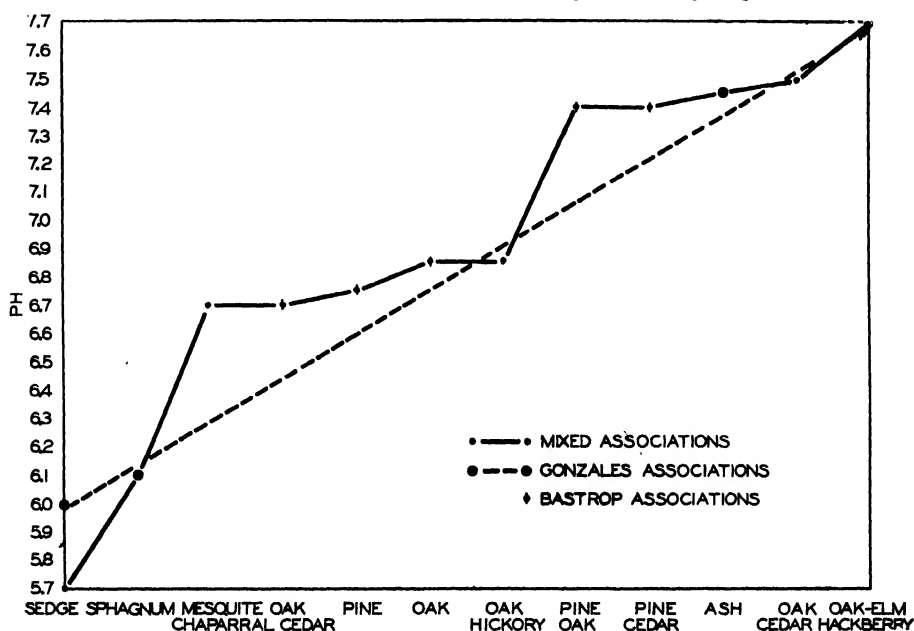


FIG. 1. The relation of plant associations to the soil reaction (surface—12 inches). Points through which short vertical lines are drawn represent associations in the Bastrop county group, all on the same geological formation.

because of root penetration and absorption, and on account of the supply of solutes reaching the superficial layers by physical means. The term, surface soil, or surface layers, includes the upper 12 inches.

If the "stations" are arranged in the order of increasing pH, we get the series from sedge to oak-elm-hackberry. The pH range extends from 5.7 to 7.7. Arrhenius ('22) pointed out that the pH limits of soils which support the growth of most cultivated plants lie between pH 4.0 and 9.0.

The pH values from the Gonzales group, as indicated by the broken line, show a less variable relation in all the associations, as a whole, from hydrophytic to xerophytic conditions, that is, with increasing dryness, the pH increases, as the plant cover varies from wet to dry.

Where many associations are concerned, as shown by the solid line, we get a variable curve, showing that other factors are involved which were not measured quantitatively.

In the Gonzales group, pH determinations of the soil of the same associates at different seasons of the year and in different years showed some variation for sedge-myrtle, ash, and oak-elm-hackberry, the variation being marked, however, for sphagnum. In all of the associations observed thus far, seasonal variations appear not to obscure those of the habitat, but further studies are in progress on these relations. Russell ('23) observed that plants cannot be sensitive to small variations, that on the whole the soil is well buffered, and that a considerable amount of acid must accumulate before any marked increase in intensity of the pH occurs. Kurz ('23) concluded that heavy rainfall, drouth periods, freezing, and thawing caused no important fluctuations in the H-ion concentration; on the other hand, Kelley ('23) observed that heavy rains lowered the acidity and drouth increased it.

The results on the Bastrop group, all on the same geological formation, are more variable than those of the Gonzales group, due probably to slopes, leaching, burning, run-off, and the like. Pine-oak has a pH which is neither like pure pine nor pure oak, nor like pine or oak when co-dominant with other species. In this particular case the higher pH value is probably due to the mat of pine needles having been destroyed by a recent fire, thereby permitting aeration and adding ash to the surface soil layers (Berkman, '28).

It is to be noted that post oak-blackjack, as dominants, and associated with hickory, occur at about pH 6.85, while live oak occurs in more alkaline soil at pH 7.5. Pine as a dominant occurs at pH 6.75. Oak-cedar, where the oak is live oak, occurs well above neutrality, at pH 7.5, while post oak-blackjack with the same cedar is found well below, at pH 6.7. Myrtle in the sedge associates appears to be limited to soils of high acidity, the occurrence in Bastrop and Gonzales counties being the farthest inland and westward that this species has been observed. Sphagnum is exceptional, since it may show a reaction near neutrality at some seasons of the year, while at others, considerable acidity, but it has been observed that the acidity of a

sphagnum bed is not far reaching either vertically downward or laterally away from the mat (Kurz, '23).

The points in the curve in fig. 1 represent, not single determinations, but values from different points in the same association. The pH values agree very closely, indicating an intimate relationship between plant cover and H-ion concentration. This observation is in close agreement with that of Olsen and Atkinson (Kurz, '23), Salisbury ('22), Arrhenius ('22), and Wherry ('20a), who considered H-ion concentration important in the distribution of species.

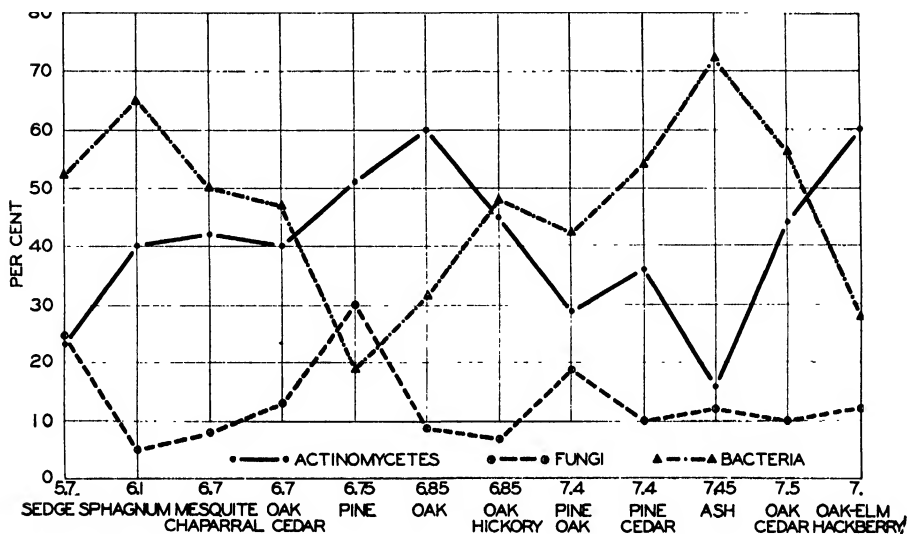


FIG. 2. The relation of plant associations to the relative numbers of actinomycetes, fungi, and bacteria.

Figure 2 shows the relative numbers of actinomycetes, fungi, and bacteria for the different plant associations. It was found that the comparison of the percentages of the different groups to the total number was more significant than the comparison of actual numbers (Snow, '26). The numbers are variable, the maxima for actinomycetes occurring at pH 6.85 (post oak-blackjack) and 7.7 (oak-elm-hackberry); for fungi, at 5.7 (sedge-myrtle) and 6.75 (pine); for bacteria, at 6.1 (sphagnum) and 7.45 (ash). In general, the number of actinomycetes varies reciprocally with both bacteria and fungi.

The relative numbers of the groups do not vary with the acidity. When the associations are favorable for one group, and not for the other, that is, where the number of bacteria is high, and the number of actinomycetes is correspondingly low, there are possibly other "significant variables" (Allen, '29) than pH. Aeration is probably the limiting factor in the occurrence of actinomycetes, a low number being found in poorly aerated sedge, sphagnum.

and ash soils. Waksman and Curtis ('18) found three and one-half per cent actinomycetes in soils which were under water part or all of the year. Moisture may be the limiting factor in the case of bacteria, the numbers being low in pine and oak-elm-hackberry associations and high in sedge-myrtle, sphagnum, and ash associates.

Pine appears especially favorable for fungi, high percentages being observed throughout the Bastrop section, where pine is a dominant. Hagem (Salisbury, '22) found fungi in abundance in the upper layers of pine forests, while Salisbury ('22) concluded that forest soil typically contains large numbers of fungi. Waksman ('24) found that forest soils sometimes contain as many fungi as bacteria.

The total numbers of organisms per cubic centimeter of air dry soil run from about 1,500,000 (sedge-myrtle at 12 inches in Bastrop county) to 23,000,000 (oak-hickory at 4 inches in Bexar county), (Table I). Of these numbers, actinomycetes make up 0 (sedge-myrtle at 12 inches in Gonzales) to 63 per cent (oak at 4 inches in Bastrop county); fungi, 0 (sphagnum at 12 inches) to 54 per cent (pine at 4 inches); bacteria, 8 (pine at 12 inches) to 80 per cent (sedge-myrtle at 12 inches in Gonzales county). Waksman and Curtis ('18) found 3-46 per cent actinomycetes, although they observed a higher per cent in soils of high undecomposed organic content. Snow ('26) found an average of 54.4 per cent for all depths, an average of 46.8 per cent being yeasts and bacteria. Waksman ('24) found that cultivated and non-acid soils contain large numbers of fungi, about 1 to every 10 bacteria, and that in forest and acid soils, an average of from 1 to 5 or 6.

Figure 3 shows the relation of micro-flora to depth; that is, the relative numbers of actinomycetes, fungi, and bacteria at 12 and at 4 inches. At unity (1.0) there are equal numbers at the two depths, above unity, greater numbers at 12 inches, and below, at 4. The horizontal line at 1.0, then, not only represents unity for the numerical values but shows the relation between the different groups at 4 and 12 inches.

A comparison of the pH at the two depths showed a close relation of the pH at 12 to that at 4 (Table I). The fact that the pH value is closely related to the plant cover, as illustrated in fig. 1, shows that the plant cover is significant, at least to a depth of 12 inches.

Considering that the pH relation at 12 and 4 inches is near unity, a direct relation between micro-flora and pH would be practically a horizontal line. Figure 3 shows a great variability. The relative numbers of actinomycetes are greater at 12 than at 4 inches in all associations up to pH 6.75 (pine); approximately equal at 6.85 (oak and oak-hickory); greater at 4 than 12 from 7.4 (pine-cedar and ash) to 7.7 (oak-elm-hackberry). From this it appears that the number of actinomycetes increases with depth in soils of pH 5.7-6.75, is about constant at pH 6.85, and decreases above this figure.

In pine, which is favorable for fungi, as shown in fig. 2, the actinomycetes are largely confined to 12 inches. In pine-cedar where the number of fungi

is low, actinomycetes are more abundant in the surface than in lower levels. This suggests that favorable conditions for fungi mean favorable conditions at the surface and competition at this level. Unfavorable conditions for the growth of fungi largely obtaining at the surface is equivalent to higher numbers of actinomycetes.

Considering the curve of fungus distribution, there is a striking reciprocal relation with that of actinomycetes, which is not obscured by smaller variations, thus from pH 5.7 to 6.85, the number of fungi is greater at 4 than at

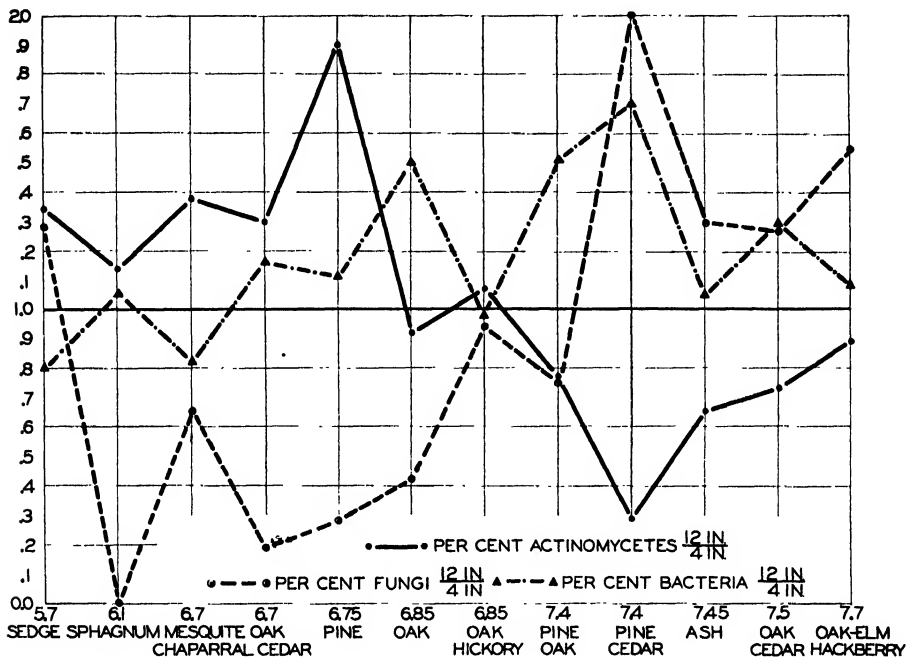


FIG. 3. The relation of micro-flora to depth. Numbers in the vertical column show numerical values.

12 inches. Actinomycetes stand in reverse proportion. From pH 7.4 to 7.7, the opposite relation holds, that is, the number of actinomycetes increases at upper levels. The number of fungi decreases.

Aside from variability, there is an evident tendency for bacteria to increase at 12 inches as compared with 4, with increasing pH 5.7 to 6.7, the numerical values being slightly below unity, and for the higher pH values, slightly above. In Tuscon soil Snow ('26) found a larger number of bacteria in the 12 inch stratum, a smaller number at 6 inches, and correlated with the greater number at 12 inches was the more nearly neutral soil reaction. From fig. 3 there can be seen in general an increase in relative numbers of fungi at 12 inches with increase of pH, a similar but slower increase of bacteria, and a decrease of actinomycetes.

SUMMARY

Determinations of the pH, and counts of the micro-flora, were made on soil samples from several plant communities in south central Texas differing significantly from the general vegetation in which they occur. Samples were taken from depths of 4 and 12 inches.

The pH values determined for different habitats with the same plant cover agree very closely, indicating an intimate relationship between plant cover and hydrogen-ion concentration. The pH at the two depths studied varies little for a given habitat, the relation of pH to the plant cover being significant at least to a depth of 12 inches. *Quercus stellata*-*Q. marylandica* as dominants occur at about pH 6.85, *Q. virginiana* at 7.5, and *Pinus taeda* as a single dominant at pH 6.75. *Morella cerifera* appears limited to soils of high acidity. Sphagnum may show a reaction near neutrality at some seasons of the year, while at others, considerable acidity. The relative numbers of the different groups of micro-flora do not appear to vary with the acidity. Aeration and moisture are probably factors here. High percentages of fungi are found where pine is dominant. High percentages of actinomycetes are found generally in the mesophytic associations, and high percentages of bacteria in marsh soils, where a small percentage of actinomycetes is the rule. The range of the total numbers of organisms is from about 1,500,000 to 23,000,000 per cubic centimeter of air dry soil; of this total, 0-63 per cent are actinomycetes, 0-54, fungi, and 8-80, bacteria.

These correlations, so far as the present study justifies, show that soil reaction and micro-flora are edaphic factors of consequence in relation to the plant cover, and to the character of the soil. The unique advantages of these areas in which edaphic factors are critical are being utilized in further studies.

The author wishes to acknowledge the helpful suggestions of Dr. I. M. Lewis, Dr. B. C. Tharp, and Dr. G. W. Goldsmith.

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FURTHER STUDIES ON DECIDUOUS FOREST ANIMAL COMMUNITIES¹

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INTRODUCTION

The tract of elm-maple forest northeast of Urbana, Illinois, and owned by the state university, has been the field of a number of quantitative studies in animal ecology by Weese ('24), Blake ('26) and Smith (1928, 1930). The present investigation covers the period from March 9 to June 1, 1925, intervening between the close of the published work of Blake and the beginning of that of Smith.

SCOPE OF WORK

This study was continued from the same stations and using the same instruments and collecting methods employed during the preceding fall and winter. Weekly thermograms were taken at 0.6 m. (low shrub level) and 11 m. (tree level) above the forest floor, and at 10 cm. (top-soil level) below it. At the height of 0.6 m. a weekly hygrogram was taken also. Population samples were collected as described in the previous paper (Blake, '26).

ENVIRONMENTAL CONDITIONS

The environment, physiographic and biotic, has been fully described by McDougall ('22) and Weese ('24), and the climatic and other conditions of the months immediately preceding by Blake ('26). On March 9, the day of the first spring collection, the soil and leaf strata, frozen and covered with snow the week before, had thawed and were damp; this condition continued until April 6, when the leaf stratum had become less moist, although the soil continued so. By April 20 the leaf stratum had become slightly wet again, the soil remaining so, and this continued through May 4. From this time until the end of the study these two strata gradually dried out.

The temperature of the air 0.6 m. above the surface of the ground is shown in fig. 1, **A**.

As in the preceding part of the study, the instrument suspended 11 m. above ground (Fig. 1, **B**) shows more extreme changes. Earlier the temperature of the tree stratum rose enormously above those of the lower levels, because the instrument suspended in the branches, as yet leafless, received the full effect of the sun during a series of warm weeks, while the other

¹ Studies from the Department of Zoology, The University of Nebraska, No. 167.

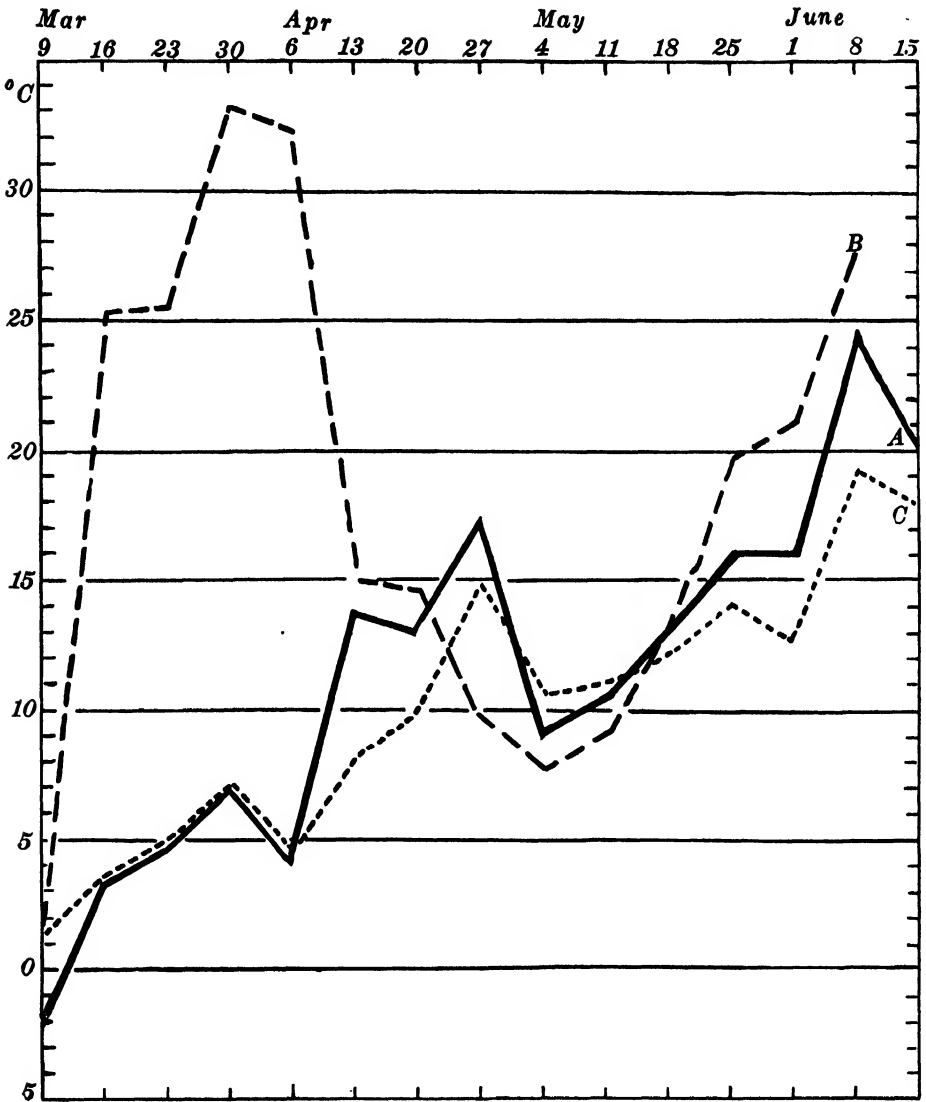


FIG. 1. Weekly mean temperatures at various strata of the deciduous forest habitat: 15 cm. below the surface of the ground, 0.6 m. and 11 m. above the surface.

All temperatures are degrees C., with a base at -5° , and horizontal ruling, 0° , 5° , 10° , 15° , 20° , 25° , 30° , respectively. Each degree is indicated by a smaller division on the margins.

The mean temperatures for the weeks ending March 9, 16, 23 and 30, April 6, 13, 20 and 27, May 4, 11, 18 and 25, and June 1, 8 and 15, are indicated by the labels and divisions on the shorter margins.

A = Temperature .6 m. above ground; B = Temperature 11 m. above ground; C = Temperature 15 cm. below ground.

instruments were in a measure protected from this by their position. During the latter part of the study, when the forest crown was putting on leaf, the temperature differences between the upper and lower strata were less marked although always more extreme at the higher station. In general, the temperature at tree level was lower with falling temperatures, higher with rising ones, than that at low shrub level. Two reversals between these strata were therefore noted, one during the week ending April 27 with falling temperatures, and one during the week ending May 25, with rising ones.

As is usually the case, the soil temperature (Fig. 1, C) was the most constant of the three.

A study of the curves of the temperature ranges (Fig. 2) indicates, as in

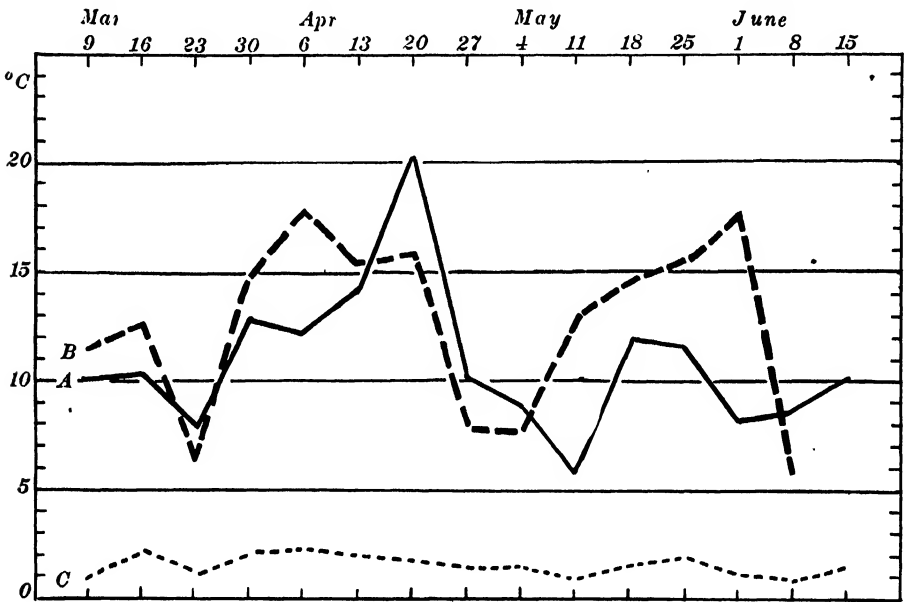


FIG. 2. Weekly mean variations of temperatures at various strata of the deciduous forest habitat: 15 cm. below the surface of the ground, 0.6 m. and 11 m. above the surface. Scheme of representation same as in preceding figure. The base-line is at 0° C.; horizontal rulings indicate 5°, 10°, 15°, 20° and 25° C. A, B, and C same as in Fig. 1.

the winter study, great relative stability of the soil temperature as compared with those of the two superterranean strata. These last show a good deal of crossing, although the general range is somewhat greater in the tree stratum, as might be expected. The lack of sharp distinction between the ranges in the two upper strata is no doubt due to constant differences in relative shading of the instruments recording them, correlated with continuous changes in the spring growth of the various stratal societies forming the plant association.

The curves showing weekly mean relative humidity and weekly mean

variations of this factor (Fig. 3) are self-explanatory. As stated in the preceding paper, the changes noted are probably of less importance in directly affecting the animal population at this time of year than as indicators of the general conditions, and particularly of the amount of moisture in the

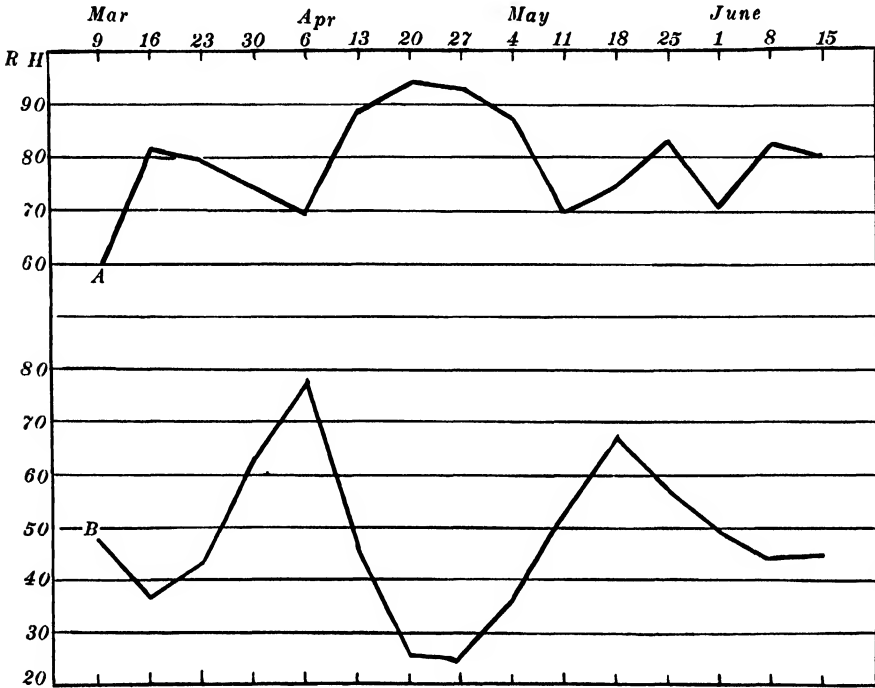


FIG. 3. Weekly mean relative humidity and weekly mean variations in relative humidity 0.6 above ground in the deciduous forest habitat.

Divisions on the upper and lower margins indicate the weekly intervals. Horizontal rulings are placed at each 10 per cent relative humidity, with base-lines drawn at 50 per cent for the weekly mean relative humidity, and at 20 per cent for the weekly mean variations in relative humidity.

A = Weekly mean relative humidity; **B** = Weekly mean variations in relative humidity.

leaf and top-soil strata, whose animal societies are directly exposed to contact with the wet substratum during periods of high atmospheric humidity.

ANIMAL SOCIETIES

The animal population (Fig. 4, **A**) rose from a fairly low point during the cool week of March 9 to the highest point attained in this study during the week of March 23. This accompanied a rise in temperature and a continued moisture of the substratum. By April 6 the total animal count had fallen off again to a point not much higher than that found at the beginning. There was a slight fall in temperature during this week, and some

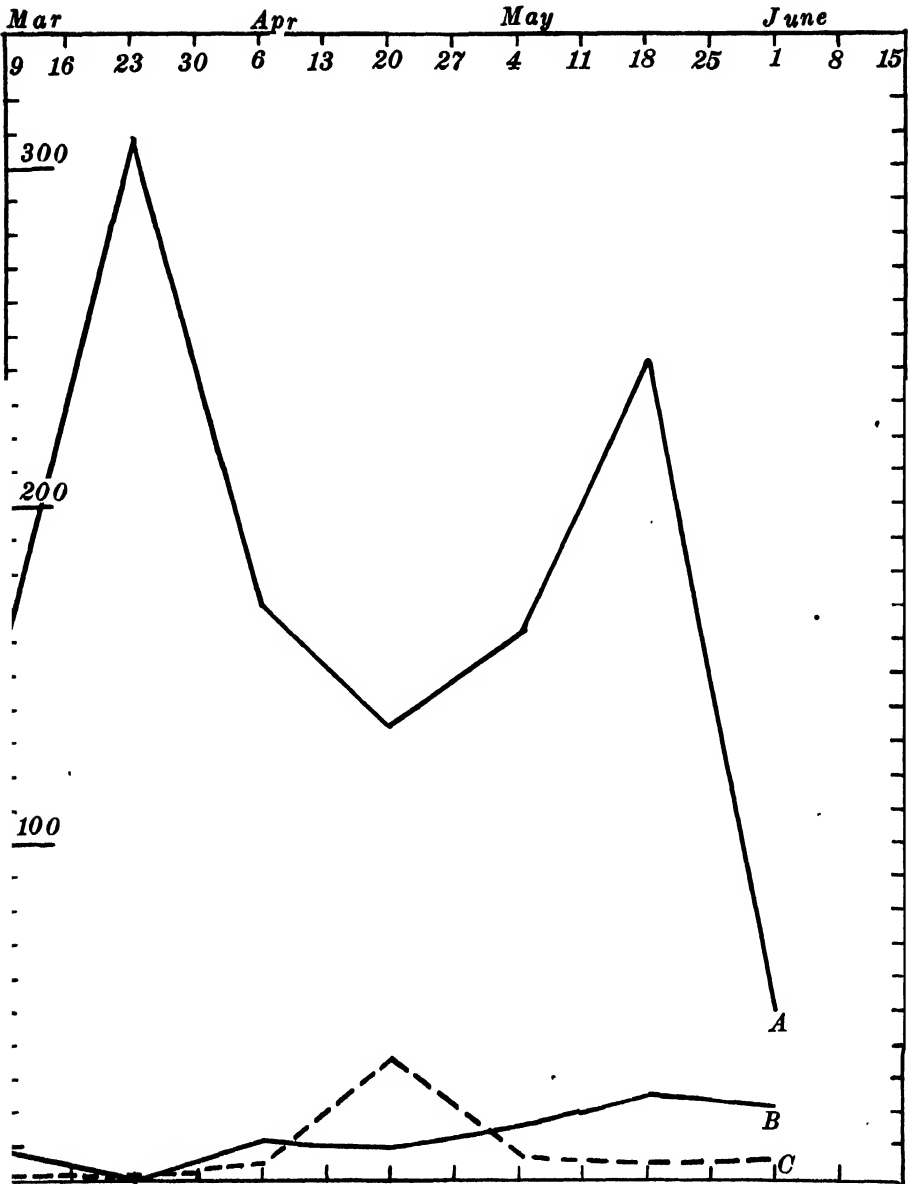


FIG. 4. Animal population, as a whole and by the two upper strata considered, in deciduous forest, March 9, 1925, to June 1, 1925. The divisions along the upper and lower margins represent the weeks, as indicated. The divisions along the lateral margins indicate 10 animals taken in collecting.

A = Total population; B = Population of herb stratum; C = Population of shrub stratum.

degree of drying of the humus layers. By April 20, when there was a still further population decrease, another slight fall in temperature had occurred; the substratum was somewhat moist. From this point the count again mounted, and by May 4 was about the same as at the start; temperatures were falling but the forest floor remained moist. On May 18 the population had increased still further, accompanied by rising temperatures in all strata. Thence the number of animals fell off sharply to June 1, the last day of population sampling; this was a week of arrested rise in temperature of the lower strata, accompanied by considerable evaporation and drying out of the leaf and top-soil layers.

Considered by stratal animal societies, it will be seen that throughout this study the shrub society (Fig. 4, **C**) was numerically of little importance in its contributions to the total population curve. The most marked exception to this was noted during the week of April 20, when a sudden temporary increase in migrating hemipterans did cause this society to make a considerable contribution to the whole number of animals taken. Otherwise there were fewer animals taken from the shrubs than might have been expected, especially during the latter part of the collecting period.

The animals of the herb society (Fig. 4, **B**) were somewhat more numerous, but their numbers seem to be correlated with increase of growth of vegetation rather than with climatic fluctuations. However, their count gradually increases with rising temperatures throughout the study, but shows little or no correlation with specific changes in climatic conditions from week to week.

The animal society of the leaf stratum (Fig. 5, **A**) dominated all the other strata in point of numbers, and determined the main outlines of the total population curve. This had been the condition throughout the preceding winter, but it was somewhat surprising to find that it continued so long into the prevernal period. It is no doubt due to this fact that the population curve shows less response than might have been expected to fluctuating climatic changes, save as these changes affected the dead leaf covering of the forest floor. In general, the population of this stratum shows two high points, correlated with rising temperatures and abundant moisture, and several low points, which accompany low temperatures or drying of the leaf layer, or both.

The population of the soil stratum (Fig. 5, **B**) was relatively the most constant, as was the case during the winter. It increased somewhat with the rising temperatures of the early weeks, and later became subject to a series of minor fluctuations which are correlated with changes in the count of the leaf society; they indicate vertical migrations in response to changes in the condition of the leaf stratum, which was directly exposed to atmospheric fluctuations of temperature and moisture. Thus increase in soil

population appears to be correlated with decrease in leaf population and *vice versa*. During the winter the upper 10 cm. of soil did not serve as a refuge for leaf stratum animals during unfavorable conditions; if driven down by cold, for example, they went *below* the 10 cm. line. But during the milder prevernal conditions, there seems evidence that many forest floor invertebrates migrate up and down between the leaf and top-soil layers, as conditions therein dictate.

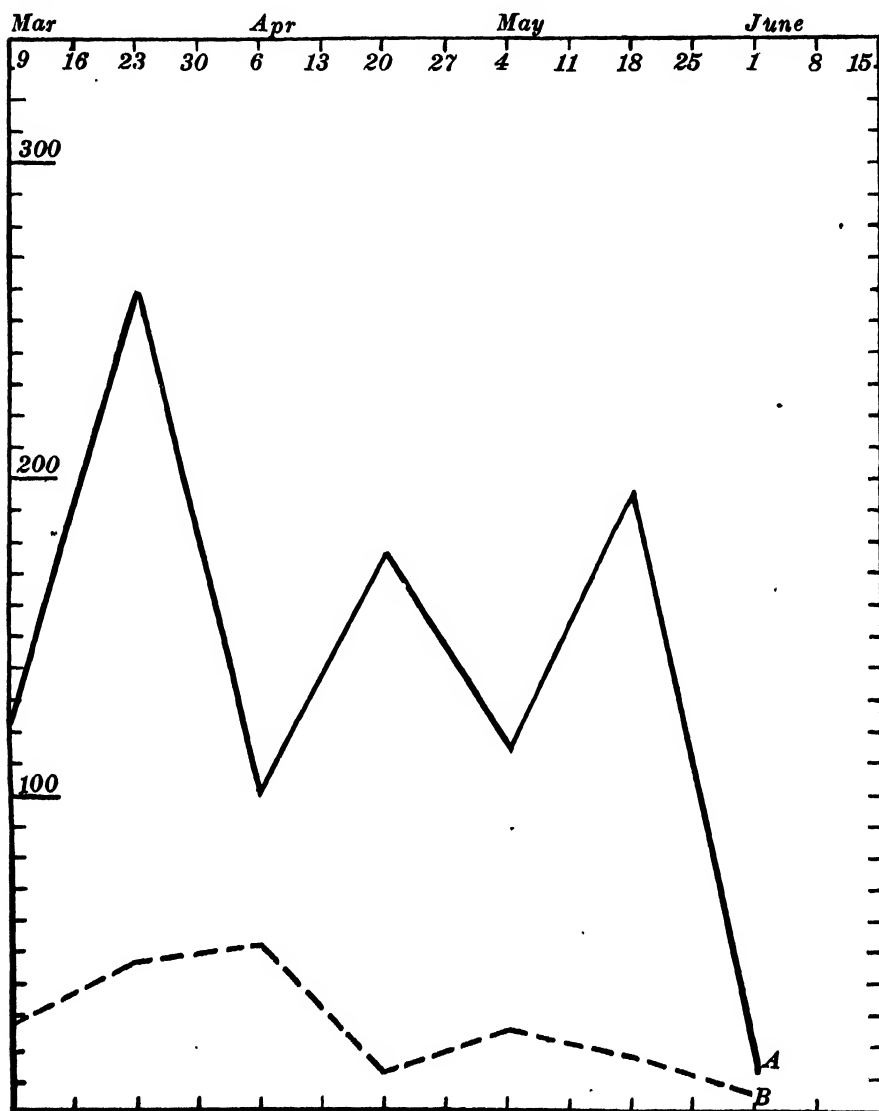


FIG. 5. Animal population of the two lower strata in deciduous forest, March 9, 1925, to June 1, 1925. The divisions are as in fig. 4.

A = Population of leaf stratum; B = Population of soil stratum.

Certain predominant ² animals (Table I) have been selected for particular study because of their abundance in the collections, their behavior in vertical migrations, their importance in previous studies made in this habitat by

TABLE I. *Invertebrates prominent in the prevernal and vernal animal societies of the elm-maple forest, 1925*

The animals here listed did not appear in any numbers in the samples of the preceding winter. The order indicates relative abundance.

	Stratum
<i>Striatura milium</i> (Morse)	Leaf
<i>Corythucha aesculi</i> O. and D.	Shrub
<i>Gastrocopta pentadon</i> (Say)	Leaf
<i>Lasius niger</i> L. <i>americanus</i> Emery	"
<i>Vertigo</i> sp.	"
<i>Xysticus</i> sp. (juvenile)	"
<i>Circinaria concava</i> (Say)	Soil
<i>Apis mellifera</i> L.	Herb

Weese, Smith and the author, or for a combination of these reasons. In the author's former treatment the stratal animal societies, based on the fall and winter study, were tentatively designated by the names of the animals which were most important at that time. Since, however, these animals are not the ones most prominent in the spring societies, no attempt will be made to carry out this nomenclature. Smith ('28) has classified the animals into two main groups, predominants and seasonals, but has not treated stratal societies (except of the forest crown (Davidson (Smith), '30) in any detail. Both predominants and seasonals have been subdivided by Smith into two groups, namely influents and sub-influents, based on various qualifications. Applying these tests to the writer's collections, certain species might have been designated as influent by reason of abundance, conspicuousness and effect on the habitat. This was not attempted, however, partly because the writer's work did not include an entire annual cycle and partly for other reasons, which will be discussed later.

Shrub Society

Corythucha aesculi O. and D. (Fig. 7, C)

This lace-bug was not found in the author's winter collections; it appeared suddenly in the shrub stratum during the early part of April, reaching a maximum about April

² This term was employed by the writer in his previous paper and its use is continued here for the sake of consistency. However, he regards it, and the resultant terms presociety, presocieties, *et cetera*, as unfortunate. A species that is predominant would, by the very derivation of the word, be preëminent among dominants. Yet this term has been employed for the ecologically important animals living in terrestrial habitats, where true dominance is undoubtedly held only by the vegetation; hence no animals could possibly be predominant *stricto sensu*. As used, it means merely an *animal* dominant or subdominant, with the above mentioned restrictions implied. It is difficult to see how the misleading word predominant is any improvement over such phrases.

20. After that it gradually disappeared from the samples, mounting to its summer home in the forest crown. Its behavior corresponds well with Weese's findings for this species.

Herb Society

Lygus pratensis oblineatus (Say)

The tarnished plant-bug had begun to emerge from hibernation and appear in the upper strata even before the close of the winter study. It appeared in considerable numbers through the spring; nymphs were found in the last collections made.

Apis mellifera L.

Honey-bees were numerous and active among the flowers of the herb stratum from April 6 onward. They are difficult to collect quantitatively by the methods used, but their abundance was also observed by cruising. Their numbers, as well as their direct effects on the plants through pollination (Clements and Long, '23) abundantly entitle them to consideration among the important animals of this society.

Leaf Society

Carychium exile H. C. Lea (Fig. 6, **A**, *b*, *c*)

This snail was abundant in the leaf stratum in November, but was not taken again during the winter. It was constantly present through the prevernal and vernal collections until June 1, when it was not taken. Throughout the spring it was the most abundant animal; its fluctuations appear to coincide more closely with the humidity than with the temperature curves, although the high points of the population occur with high or rising temperatures. The period about April 6 was one of drying of the leaf stratum, although the top-soil had not dried out. A slight increase in the soil population, accompanied by a decrease in that of the leaves population, is probably an indication of a temporary downward migration of this snail to escape the less favorable conditions in the dried leaves; this is in accordance with the studies made on the behavior of other snails during the previous winter. Smith lists this species as a predominant, but assigns it only secondary or influent importance as such.

Pseudovitrea minuscula (Binney) (Fig. 6, **B**, *b*, *c*)

Like the preceding species, this snail had been of considerable importance in the winter society, where it figured almost wholly as a leaf stratum inhabitant; in the present study it was the second most numerous animal, and was still found principally among the forest floor debris. It was constantly present in considerable numbers, and its fluctuation curve approaches that of *Carychium exile* and is no doubt determined by the same environmental factors. In Smith's classification this snail is assigned the same ecological status as the last named species.

Glyphyalinia indentata (Say) (Fig. 6, **C**, *b*, *c*)

This snail was also an important inhabitant of the winter society, occurring in both leaf and soil strata, but mostly taken from the former. Like the two species last named, it was a prominent animal throughout the spring collections, being more abundant in the early portion of the study when the forest floor was more damp. There was a marked rise in the soil count of this species about March 23, followed by a decrease as the animals migrated upwards into the leaf stratum during the following weeks. With the

FIG. 6. Spring populations of mollusks. **A.** *Carychium exile* H. C. Lea; *b.* Leaf stratum, *c.* Soil stratum. **B.** *Pseudovitrea minuscula* (Binney); *b.* Leaf stratum, *c.* Soil stratum. **C.** *Glyphyalinia indentata* (Say); *b.* Leaf stratum, *c.* Soil stratum. **D.** *Striatura milium* (Morse). **E.** *Gastrocopta pentadon* (Say). **F.** *Vertigo* sp. **G.** *Circinaria concava* (Say); *b.* Leaf stratum, *c.* Soil stratum.

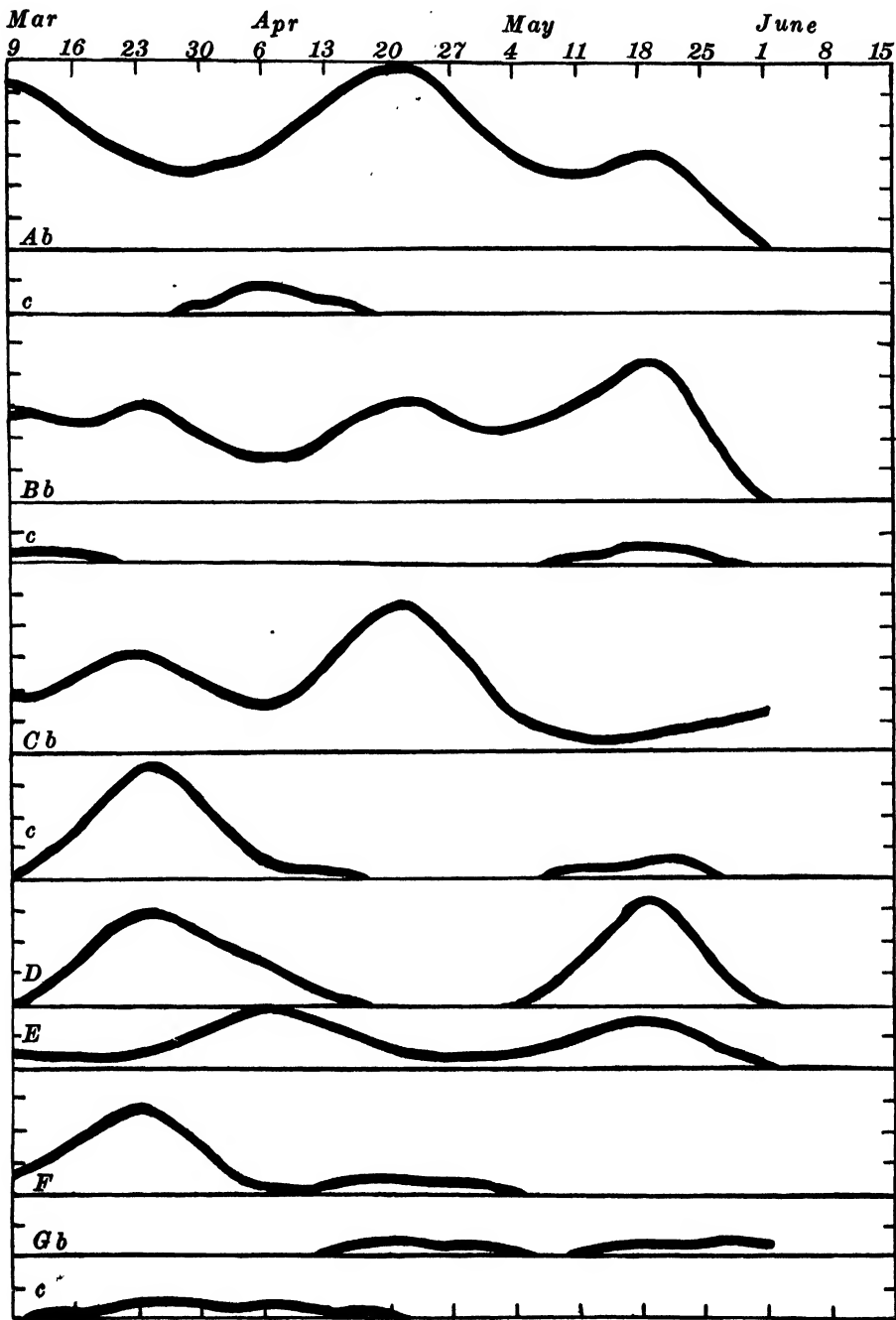


FIG. 6.

drying of the upper layer in May these snails again appeared in the soil. At the close of the study there is some evidence of another slight upward migration.

Tomocerus flavescens Tull. *americanus* Schött (Fig. 7, Bb, c)

This springtail was the most numerous animal in the leaf population of the preceding winter. Its fluctuations during the spring sampling accompany the temperature changes somewhat more closely than was the case with the mollusks, but also show some correlation with changes in humidity and consequent moisture of the lower strata; especially did it share the falling off of numbers shown by all leaf stratum inhabitants during the drying out of that layer in the latter part of the work. The temperature depression of the week of April 6 caused some downward migration into the soil, which was reversed during the weeks following. Smith lists this species as a predominant of major or influent value.

Striatula milium (Morse) (Fig. 6, D)

This snail appeared in considerable numbers at two periods in the spring study, always in the leaves. These periods coincided with rising temperatures, but the animals were absent during an intervening period¹ when the temperature also attained a high point. Like most of the other mollusks they fell off rapidly at the very end of the study, as the leaf stratum dried.

Cantharis sp. (larva) (Fig. 7, Db, c)

The larvae of this soldier beetle had occurred steadily in the winter collections and were constantly found in the present study. They were most abundant in the leaf stratum but smaller numbers occurred in the soil from time to time. Their fluctuations were not sufficient to make possible any correlation with environmental changes, but the period of their least numbers coincides with a sharp drop in temperature. Smith lists *Cantharis excavatus* Lec. as a seasonal influent of the estival society.

Gastrocopta pentadon (Say) (Fig. 6, E)

This species was constantly present throughout the spring study. It had two maxima, the second agreeing with the last maximum of many forest floor mollusks, May 18; its first maximum, that of April 6, does not agree with that of the others.

Tipula sp. (larva) (Fig. 7, E)

Crane-fly larvae, referred to this genus, had been present in considerable numbers during the winter, occurring in both leaf and soil strata. They continued in smaller but constant numbers in both strata during the spring study, rising to a peak in the leaf society of May 4. They then fell off rapidly and were not taken later.

Lasius niger L. *americanus* Emery (Fig. 7, Fa, b, c)

Black ants were occasionally swept from the herb stratum on warm days during the month of April. Numbers were taken in the leaf, and some in the soil strata, in the latter part of the study. Weese lists them as constituents of the estival society, occurring in the ground (leaf and soil) stratum. The large numbers taken about May 18 probably indicate fortuitous inclusion of groups of the species in the quadrat counted, rather than any particular increase at the time; this illustrates the discontinuous distribution of these ants on the forest floor.

FIG. 7. Spring populations of various invertebrates. A. *Enchytraeidae*; b. Leaf stratum, c. Soil stratum. B. *Tomocerus flavescens* Tull., var. *americanus* Schött; b. Leaf stratum, c. Soil stratum. C. *Corythucha aesculi* O. and B. D. *Cantharis* sp. (larva); b. Leaf stratum, c. Soil stratum. E. *Tipula* sp. (larva); b. Leaf stratum, c. Soil stratum. F. *Lasius niger alienus* var. *americanus* Emery; a. Herb stratum, b. Leaf stratum, c. Soil stratum.

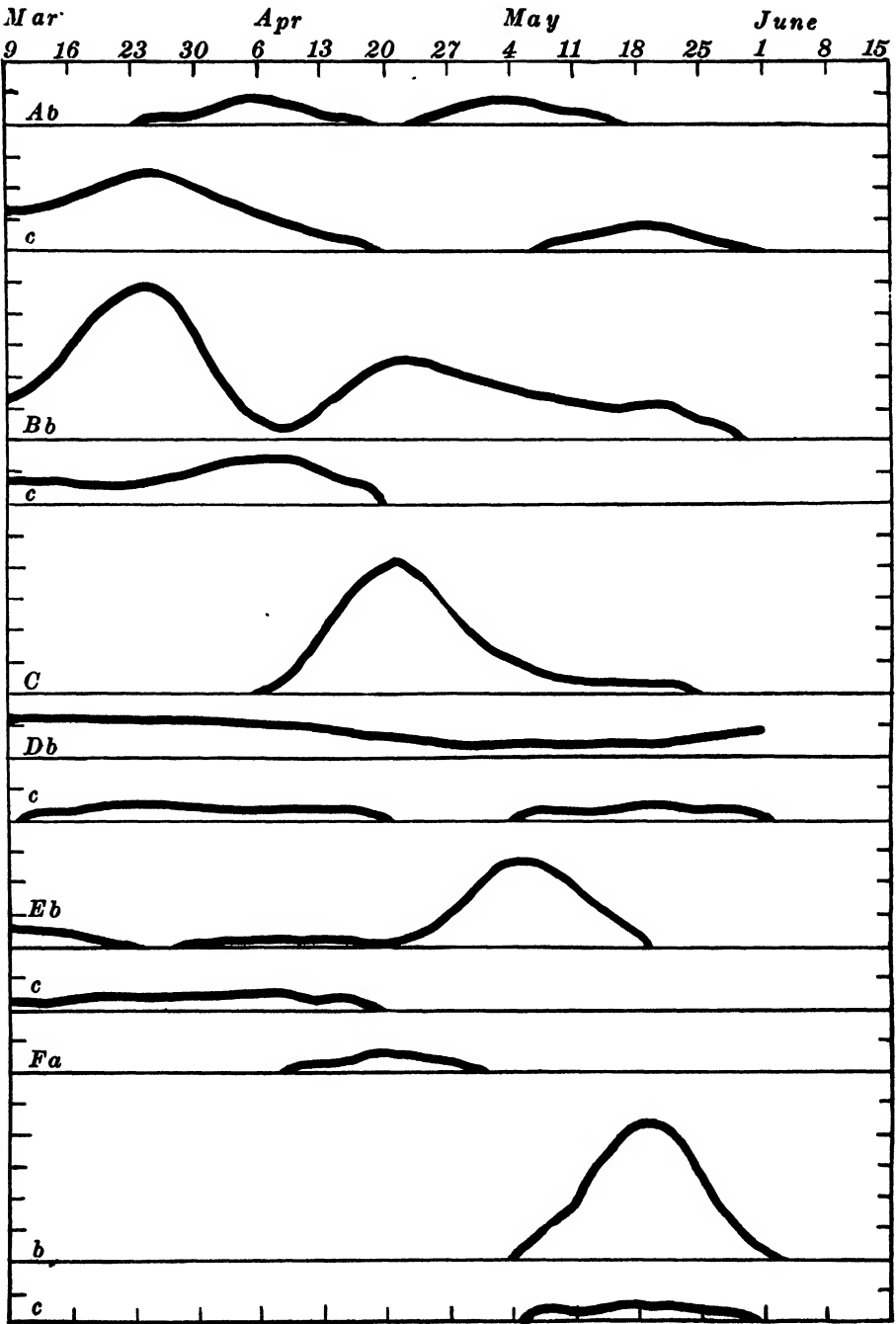


FIG. 7.

Vertigo sp. (juvenile) (Fig. 6, F)

Young snails referred to this genus appeared in large numbers in the leaf stratum early in the spring, coinciding in their maximum with a number of other mollusks. Thence they gradually disappeared, and did not take part in later maxima of this group.

Onychiurus subtenuis Fols.

This springtail became very abundant in the latter part of the winter during a period of warm, wet weather; it was a leaf society member. During the spring it appeared from time to time, usually in the leaves but rarely in the soil. Its highest point did not even approach the winter maximum for the species. Smith assigns to it status as a predominant of subinfluent rank.

Xysticus sp.

Crab-spiders belonging to this genus were constant denizens of the leaf stratum through the spring study, although never present in very large numbers; many juveniles were taken. Weese lists it as a constituent of the prevernal society at ground level, and also as occurring later in the season. Smith gives the species as an autumnal seasonal, but accords it influent status.

*Top-Soil Society**Enchytraeidae* (Fig. 7, A*b*, *c*)

Enchytraeid worms were extraordinarily abundant in the warm, wet weather of the latter part of the winter, and continued in smaller numbers through the spring. Earlier they were most prominent in the leaf society, but in the spring study there were more in the soil; there is some evidence of vertical migrations, correlated with changes in moisture. Smith lists these animals as predominants of influent value.

Circinaria concava (Say) (Fig. 6, G*b*, *c*)

This snail was present in smaller numbers than the other mollusks, but constantly throughout the period of collecting. It first appeared in the soil and thence apparently worked up into the leaf layer. It did not share to any extent in the maxima shown by other snails.

DISCUSSION

The present study, short as it is, seems of interest in filling the gap between the close of the author's winter work on March 2, 1925, and the beginning of the work of Smith at the same station. It indicates that, for this particular year, the leaf stratum animals continued in predominant numbers almost up to the end of the vernal period, so that this stratal society continued to dominate numerically the total population until nearly the close of the study. By that time, however, the leaf and soil populations were falling off and the herb and shrub populations mounting, in preparation for what is apparently the typical estival distribution of animal numbers in this habitat.

The animals present in large numbers, with few exceptions, are species characteristic of the leaf stratum. The societies of the upper strata, even when they mounted to considerable numbers, consisted mostly of comparatively few individuals belonging to many species; only three species appeared in any numbers during the spring study and one of these (*Lygus pratensis*) had been rather prominent through the winter, hibernating among the leaves. Much the same might be said of the constituents of the top-soil society.

Twelve animals were prominent in the leaf society. Seven of these had also been important in the leaf stratum during the preceding winter. Two of the others (*Lasius niger* and *Xysticus* sp.) are listed by Weese as important ground stratum animals of the spring society in 1922.

Since the mass of the animal population was found in the lower strata during the period of study, it is not surprising that the fluctuations in numbers did not coincide more closely with weekly changes in atmospheric temperature and humidity, save as these were reflected in the physical state of the substrata. In general, of course, the changes in numbers of these ground-dwelling animals agree with climatic changes, but they follow more closely the *effects* of such changes on the temperature and dampness of the forest floor debris. This agrees with findings during the winter study, when these lower societies were also the most conspicuous constituents of the total population.

As indicated by the graphs, there is a general agreement in the fluctuations of different species of mollusks, for example, from week to week. However, as was the case in the winter, there are some species whose high points do not coincide with those of the majority. This may be due to their chance occurrence in large numbers in the quadrats selected for sampling, but it may also be due to physiological differences between species, as was suggested in the preceding paper.

During the past few years there have been repeated attempts by various plant and animal ecologists to select, on a basis of quantitative samples, organisms which could be used as a basis for naming the biotic communities, seral and stratal, to which they belong. This seems to have been fairly successful in the case of plants (Clements, '28), where the species are relatively few in number and the individuals are non-motile. Likewise in the case of marine animal communities (Shelford and Towler, '25) this treatment has been employed with some success; here the animals are the dominant organisms of the entire biotic association, and many of them are sessile or relatively so.

Others, including the author, have attempted to apply similar methods to the animal communities of terrestrial habitats, where the species are numerous and fluctuating and the individuals are often highly motile and migratory. The most elaborate series of studies of this sort within the author's knowledge has been made by several investigators working in the tract of elm-maple forest which formed the field of the present study. These workers used uniform methods and made their studies in different years. It seems that it would be of more than passing interest to briefly compare their results, with a view to possible evaluation.

Three quantitative studies were made, in which the same methods, originally devised by Weese, were employed. In the order in which the work was done, they were as follows: Weese, July 4, 1921, to July 3, 1922; Blake.

October 6, 1924, to (inclusive of the present study) June 1, 1925; Smith, working in 1925 and 1926, more frequent samples being taken the latter year. In making comparisons it must be remembered that the aims and viewpoints of the three investigators were not identical, although they worked on the same ground and employed the same sampling methods. Weese evidently placed his emphasis on seasonal and stratal distribution of animal societies, and its bearing on experiments with the responses of selected species to experimental gradients of physical factors. Blake was mainly concerned with the comparison between conditions and biota in the elm-maple forest and those found in coniferous forests previously studied by him. Smith attacked the problem as a climax of the deciduous forest animal sere, studying earlier stages at the same time. Further, as Pearl ('11) long ago pointed out, different investigators working on the same data may not reach identical results, because of the personal equation involved.

Aside from these varying aims, there are other differences which make it necessary to use caution in comparing the results of these investigations. Smith draws some data from a neighboring tract of red oak-maple forest, and also made a very careful and elaborate study of the animals of the forest crown and tree trunks, not treated in any detail by either Weese or the present writer. The last, on the other hand, included a study of the winter birds and what data could be gathered on the mammals, neither of which received any extensive treatment by his co-workers. Fortunately for our comparison, both Smith's work on the upper societies and this writer's treatment of the higher vertebrates may be readily segregated from the rest of their results. When this is done, we still have the remaining data, collected by uniform methods during the years given.

Weese lists all species taken by him and designates as dominants certain species to which he gives particular treatment; aside from dividing his animals into seasonal and stratal societies, he employs no ecological nomenclature. Blake made no attempt to divide his conspicuous animals into seasonal and permanent species, but included all prominent forms under the term predominants; these were divided again into stratal societies, named tentatively after the most important animals present in each at the time the study was made. Smith, as stated above, has given us an elaborate nomenclature, according to principles which are defined.

In the following comparison, only animals which are singled out for particular treatment by two or more of the investigators will be considered. All three collections had considerable numbers of species which were represented by few individuals or were otherwise considered as of minor importance by the respective workers; these will be disregarded. Neither will any attempt be made to list the animals according to the ecological evaluation placed on each species by the different authors—an almost impossible thing to do, because of the different terminologies employed.

TABLE II. *Animals listed as of ecological importance in three surveys of the elm-maple forest,* University Woods, Champaign County, Illinois, made by three investigators working at different times*

Only animals that appear on at least two of the three lists are given here. The order is taxonomic.

	Weese 1921- 1922	Blake 1924- 1925	Smith 1925- 1926
Enchytraeidae.....		*	*
<i>Pseudovitreia minuscula</i> (Binney).....		*	*
<i>Carychium exiguum</i> (Say).....		*	*
<i>Carychium exile</i> H. C. Lea.....		*	*
<i>Dictyna volupis</i> Keys.....	*	*	
<i>Linyphia phrygiana</i> C. Koch.....	*	*	*
<i>Mangora gibberosa</i> Htz.....			*
<i>Tetragnatha</i> sp.....	*	*	*
<i>Xysticus</i> sp.....	*	*	*
<i>Anyphaena rubra</i> Em.....	*	*	*
<i>Fontaria virginiensis</i> (Dru.).....		*	*
<i>Pokabius bilabiatus</i> (Wood).....		*	*
<i>Onychiurus subtennis</i> Fols.....		*	*
<i>Tomocerus flavescens</i> Tull. <i>americanus</i> Schött.....		*	*
<i>Corythucha aesculi</i> O. and D.....		*	
<i>Lygus pratensis oblineatus</i> (Say).....	*	*	
<i>Empousca viridescens</i> Walsh.....	*		*
<i>Erythroneura obliqua</i> Say.....	*		*
<i>Cantharis</i> sp.....		*	*
<i>Notoxus monodon</i> Fab.....	*		*
<i>Epuraea rufa</i> (Say).....	*		*
<i>Telephanus velox</i> Hald.....		*	*
Phalacridae.....	*	*	*
<i>Diabrotica vittata</i> (Fab.).....	*		*
<i>Epitrix fuscata</i> Cr.....	*		*
<i>Epitrix brevis</i> Sz.....	*	*	
<i>Chaetocnema confinis</i> Cr.....	*		*
<i>Glyptina spuria</i> Lec.....	*		*
<i>Phyllotreta sinuata</i> (Steph.).....	*	*	*
<i>Phytonomus nigrirostis</i> Fab.....	*		*
<i>Leptocera evanescens</i> Tuck.....	*	*	
<i>Leptothorax curvispinosus</i> Mayr.....		*	*
<i>Lasius niger</i> L. <i>americanus</i> Emery.....	*	*	
<i>Cyanocitta cristata</i> (L.).....		*	*
<i>Peromyscus leucopus novahoracensis</i> (Fisch.).....		*	*
<i>Sciurus niger rufiventer</i> (Geoffroy).....		*	*

* Smith also drew data from a neighboring red oak-maple forest.

Keeping these restrictions in mind, a single table (Table II) will show at a glance the amount of overlapping between the lists. Weese lists 35 species of sufficient importance to merit particular mention, Blake 54 and Smith 59. Of these, 36 species appear on two or more of the lists, and these alone are given here. Of Weese's 35 species, 23 are in agreement with one or both of the other lists: 6 with Blake, 10 with Smith and 7 with both. Of Smith's 59 species, 30 are included in one or the other list: 13 coincide with Blake, 10 with Weese and 7 are common to all three lists. Only 7 animals are common to all, 5 spiders and 2 beetles, one of the latter determined to family only. It is evident, then, that there is not a large

amount of *absolute* agreement between the three lists. Further it will be seen that, although Weese and Smith collected through an annual cycle and Blake only through the fall, winter and spring, the lists of the first two workers do not agree with each other conspicuously more than they do individually with the latter; they possess 17 species in common, while Weese and Blake have 13 in common, and Smith and Blake have 20 in common.

On the other hand, a glance at the table will indicate that there is a very considerable amount of *general* agreement, since all the 36 species listed were important numerically or otherwise in two of the collections. The agreement might be even closer if the author's collecting period had included an estival society, the absence of which no doubt is the cause of the failure of his list to coincide more completely with the other two. The agreement between his list and that of Smith is mainly in more or less permanent inhabitants of the lower strata. The same applies to the relations between his work and that of Weese, save that here the forest floor forms occurring on both lists are mainly hibernating animals of the winter society, whose estival activity takes place at higher levels. On the other hand, the overlapping between the lists of Weese and Smith is largely in the case of insects of the estival and serotinal societies, presumably collected from the vegetation. It seems to the writer that the results of this comparison cannot fail to give us a more reliable concept of the real aspect of the animal communities than any single study can do. The species that appear on two or more of these lists are of much more importance to us than the others, however conspicuous at the time of study, which failed to appear in one or the other of two studies made at different times on the same ground.

The author is less sanguine on the application of a detailed nomenclature to terrestrial animal communities and their constituents, in the present state of our knowledge. He feels that his own previous attempts to apply such a nomenclature, as well as the attempts made by others, have been premature. Stratal and seral communities have been named on the basis of animals predominant in them at the time of study; but these species may fail to appear in important numbers and relations in a similar study made on the same ground at a different time. Based on this comparison, any single year's study cannot be relied upon to give results that agree in great detail (*i.e.*, species by species) with that of another year, even in identical habitats. Until we have a considerable amount of comparable data, giving us a picture of the fluctuations of the same species from year to year, we are hardly justified in using such species as "handles" to name the communities in which they occur, no matter how abundant or important these species may be at the time of our study. Therefore no attempt has been made in this paper to name the stratal societies by their prominent animals, as was done in the earlier investigation.

Likewise the matter of distinction between predominants and seasonals.

and between influents and sub-influents, is one where much caution may well be observed. Unless we are to restrict the seasonal activity of insects, for example, to the presence of the adults in the upper strata, certain forms now classed as seasonals would certainly become predominants. But are we justified in withholding the term active from larval stages? In one of the studies quoted, a soldier beetle, *Cantharis excavatus*, is listed as a seasonal estival, although larvae, presumably of this species, were conspicuous in the lower strata throughout the fall, winter and spring collections. Unless we are prepared, by very definite life history studies, to evaluate the relative effects on the habitat of a species at different periods in its life cycle, it is difficult in many cases to apply this distinction between predominants and seasonals. The same applies, and with even greater force, to the distinction between influents and sub-influents. The rank of two animals of similar habits, such as two snails, springtails or closely related beetles, would of necessity depend on numbers alone. And the evidence given by the comparison of the three studies mentioned tends to show that the influent or sub-influent value of two such species might be reversed in different years, owing to annual fluctuations. Thus species listed as having very definite ecological value in one of these papers, did not appear at all, or appeared as of very minor value, in the others.

The writer would not wish to go on record as opposing a rational classification of animal communities and their constituents, based on quantitative studies. He was himself one of the earlier workers in this field and has erred as much as anyone in the matter of attempting terminology based on relatively short-time studies. The comparison given in this paper seems encouraging, and to indicate that the workers with quantitative sampling are on the right track, if only they will not be too hasty in attempting to generalize from their results. The collection of quantitative data on terrestrial animals, and their comparison through a number of years, should eventually give us an excellent index to the whole community problem. When such data have been accumulated they may well serve as a basis for a terminology that will in itself state the seral and stratal relations of the prominent animals. But we have not as yet the foundation for developing and applying such a system to terrestrial animals, save in the most general terms. In the meantime we are not justified in attempting to carry out, to five places of decimals, a nomenclature designed to express the as yet somewhat more than problematic relations of particular species to the community as a whole.

SUMMARY

The field work was done in the spring of 1925; the period covered is from March 9 to May 25, closing a gap between two published studies. Quantitative population samples were taken at different levels, and meteorological data recorded at corresponding stations. During most of the period, the

leaf stratum animals were the most numerous and determined the total population curve; towards the close, leaf and soil animals were decreasing and herb and shrub species increasing. Population changes accompanied meteorological changes or the effects of such changes on the substratum; numbers rose with high temperatures and increased moisture, and fell with the reverse. Since a large proportion of the population was forest floor invertebrates, especially mollusks, substratal moisture sometimes over-rode atmospheric temperature in effect. A few species, not prominent in the fall and winter collections, appeared in considerable abundance. The author's studies in this habitat include 54 species of some ecological importance; Weese, using the same methods on the same ground in 1921-1922, lists 35 such species, and Smith, in 1925-1926, 59. Of these, 36 species appear on two or more of the three lists; only 7 appear on all three. It would appear that we should not be over-hasty in using single studies of not more than a year's duration as a basis for any detailed ecological nomenclature of the communities in question.

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ECOLOGICAL SURVEY OF A FLORIDA SCRUB

MAURICE MULVANIA

In Charge Ecological Research, Mediterranean Fruit Fly Eradication

Botanically, the Florida "scrub" is one of the most interesting and weird of plant associations. Economically, the plants, as well as the soil, have almost no importance. The nearly pure white sand of the ground surface, when viewed from a short distance, gives the impression of a thin rift of wind-driven snow. The vegetation is mostly dwarfed, gnarled and crooked, and presents a tangled, scraggly aspect. It appears to desire to display the result of the misery through which it has passed and is passing in its solution of life's grim riddle. Here live the rosemary (*Ceratiola ericoides*),¹ spruce pine (*Pinus clausa*), poor grub (*Xolisma ferruginea*) and their associates rooted in a bed of silica, to which the term soil is but remotely applicable. Here the sun sheds its glare and takes its toll of the unfit.

In connection with the campaign against the Mediterranean fruit fly in Florida, 1929-30, a great many ecological plant surveys were made in various parts of the state by O'Neill and his associates; the work here reported was an intensive study of a small section of the broad field somewhat hastily covered by them. Three types of plant associations were considered in the study, but results secured on the scrub only are given here.

The scrub association was recognized as a distinct type of vegetation in the early floristic and soil studies of Florida, and was probably first described by Vignoles (1823). It was, however, overlooked by Williams (1827) and Smith (1884) in their discussions of the soils and vegetation of the state. Nash (1895) distinguished 5 floral areas (high pine) land, scrub, low pine land, bayheads, and hammocks), and described in some detail the vegetation of each. He concluded that a definite antagonism existed between the plants on the scrub and the adjacent high pine, and called attention to the fact that there is no intermingling of the species peculiar to the two associations. He lists a few of the more abundant forms on the scrub, and notes the complete absence of grasses. Nash made the very interesting observation that scrub vegetation has no special provision for the prevention of death by fire. The high pine plants generally have some means of avoiding such a fate. Whitney (1898) briefly compares the high pine vegetation with that of the scrub, emphasizing the sudden transition from one to the other, and states that from chemical and physical analyses there is no manifest reason for the difference observed. The topography is likewise dismissed as a factor.

¹ Plant names from Small, J. K. *Flora of the southeastern United States*. 2d edition, New York, 1913.

He suggests that the difference in the character of vegetation is accidental, one type getting started first and holding the ground. It is said that the same character of vegetation that is found on the typical scrub soil extends to the lake borders into the muck-like soil. A table of moisture content on the scrub and high pine soils for April and May, 1896, shows a slight excess in favor of the scrub in April, but this order is reversed in May, and he concludes from these figures that water is not the controlling agent. Harper ('14a), in discussing the habits of coniferous plants, mentions the preference of the spruce pine (*Pinus clausa*) for the excessively poor soil of the scrub and old coastal dunes and notes its association here with *Quercus geminata*, *Q. myrtifolia* and *Serenoa serrulata*. Harper ('14b) observed that the coastal "stationary" dunes are forested by pines and evergreen shrubs mainly, indicating an exceedingly poor soil. Forest fires generally pass through these forests and destroy *Pinus clausa* about once in the lifetime of the trees. These are soon replaced by seedlings. Harper ('15) notes a close correlation between the scrub vegetation in Marion and Citrus Counties, Florida, and the white soil "almost devoid of humus and animal life." This soil is said to consist of perhaps 98 per cent silica. He lists what he considers a representative scrub vegetation of the counties mentioned above. Harper ('21) shows by photographs the manner of reforestation of the scrub after the ravages of fire. In discussing the white and cream-colored phase of the deep sandy soils (supporting the scrub and high pine vegetations, respectively) he states that the white sand is very poor in potash, clay, humus, and animal life, as compared with other soils of the locality, and supports generally a scrub vegetation where the elevation is high, but may support a flatwoods vegetation if it occupies a low and flat position. The cream-colored sand, on the other hand, has from 3-8 per cent silt and clay and a higher content of potash, lime, magnesia and phosphoric acid, especially the latter. His chemical analyses were taken from Whitney (1898). He states that the typical scrub is peculiar to Florida, but is similar to that of other regions having poor soil or deficient rainfall. In the 17th annual report of the Florida State Geological Survey, Harper ('26) makes the observation that the deep white sand is remarkably free from burrowing animals, while the adjacent yellow phase is very well inhabited by such animals, as salamanders, gophers, ants, etc., which probably do much to keep the soil stirred up. In the 18th annual report, Harper ('29) gives a fairly complete list of the species of plants found on scrub soil. The list includes rather more forms than are likely to be seen on any one area.

In a general way, the scrubs may be referred to as the dunes or coastal scrubs and the interior scrubs. What appear to be the newer associations are close to the coast (especially the east coast of the state) and the soil reveals a comparatively recent dune formation, often richly supplied with intact calcareous shells, and has an alkaline reaction. The older or interior scrubs occupy the central portion of peninsular Florida. Disintegration of

whatever shells may have been present is complete, and leaching through an evidently long period has left only an almost pure silica sand with an acid reaction. On the inland scrubs the vegetation has become stabilized and is generally comparatively uniform throughout the highland region of the peninsular ridge. The coastal scrubs are rather less uniform in their vegetation.

The area covered by the survey here indicated comprises a typical interior scrub association, and lies between a roadway and lake near Windermere, Orange County, Florida. It consists of a rectangle, 100 by 450 feet. This terrain was laid off into 5 rectangular sections, 4 of which were square and contained 10,000 square feet each; a 5th section, 50×100 feet, covering 5,000 square feet. These primary divisions were subdivided into eight equal triangles in the case of the 4 larger plots, and 4 similar triangles in the case of the 5,000 foot plot. The diagram appended to Table I shows the manner of platting and identifying the various areas. It is seen that each triangle covers an area of 1,250 square feet. The plants on these areas were counted and listed in such a way as to make it convenient to compare directly any equal areas on any of the plats. No account was taken of the lichens; they were so numerous, both epiphytically and terrestrially, that the task of counting appeared out of proportion to their importance as members of the association.

Analysis of the results shows that the vegetation on Plats I, II and III is fairly uniform, both as to kinds and numbers. These plats have practically

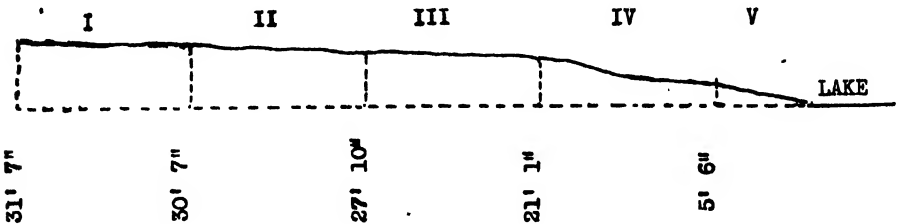


FIG. 1. Transect of scrub prospect, showing elevation above the lake level.

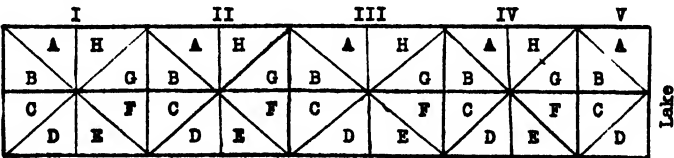
the same elevation, as shown by figure 1. The exposure and the soil, at least to a depth of 8 feet, are also uniform. On the other hand, Plats IV and V show a marked vegetational dissimilarity as compared with I, II and III. This difference is apparent in the accompanying pictures (Figs. 2 and 3) showing sections not more than 50 feet apart, figure 2 being taken on Plat III, and figure 3 on Plat IV. Plat IV contains 5 species which do not appear on either I, II or III, and Plat V has 9 which are not on I, II or III. On the other hand, Plat I contains three species not on IV, and 4 not on Plat V. There is also a very noticeable change in the numbers of plants which are common to all the plats.

In seeking an explanation for the change of vegetation seen in passing

from Plat III to IV, several ecological factors received attention, particular emphasis being placed on water relation, visual appearance, and reaction of the soil and subsoil. In Florida, and peninsular Florida especially, most of the native plants are in a vegetative condition practically the year round. During the mid-winter season, rainfall being small, the water supply is very scant and many plants receive a deficient amount. The areas, therefore, least capable of retaining moisture in the region occupied by the plant roots

TABLE I. *Plants found on scrub near Windemere, Florida.*
Below the table is a diagram showing the arrangement of the plats.

Kinds	Names	No. of each species on					
		10,000	10,000	10,000	10,000	5,000	Total
		sq.ft.	sq.ft.	sq.ft.	sq.ft.	sq.ft.	
		I	II	III	IV	V	
Trees	<i>Tamala humilis</i>	54	60	25	72	127	338
	<i>Pinus clausa</i>	4	17	13	24	2	60
	<i>Tamala borbonica</i>					3	3
	<i>Osmanthus americana</i>				1	1	2
Shrubs	<i>Xolisma fruticososa</i>				625	446	1071
	<i>Vaccinium nitidum</i>	14	8	2	699	186	909
	<i>Quercus geminata</i>	14	161	263	321	64	813
	<i>Xolisma ferruginea</i>	258	27	10	362	112	769
	<i>Sabal etonia</i>	35	202	411	34	8	690
	<i>Serenca serrulata</i>	88	43	159	206	67	563
	<i>Ilex glabra</i>				5	469	474
	<i>Ceratiola ericoides</i>	128	177	139	4		448
	<i>Quercus myrtifolia</i>	109	10	35	38	13	205
	<i>Smilax beyrichii</i>	29	35	31	65	29	189
	<i>Quercus chapmanii</i>	91	3	35	38	9	176
	<i>Carberia fruticosa</i>	30	21	30	60	21	162
	<i>Ximenia americana</i>	31	22	58	22		133
	<i>Ilex caroliniana</i>			12	4	86	102
	<i>Polycodium neglectum</i>	9		11	60		80
	<i>Pteridium aquilinum</i>				12	57	69
	<i>Geobalanus oblongifolius</i>	65					65
	<i>Prunus geniculata</i>	15	9	11	2		37
	<i>Bejaria racemosa</i>				20	17	37
	<i>Morella cerifera</i>					36	36
	<i>Ascyrum hypericoides</i>					18	18
	<i>Opuntia austrina</i>	7	6	3			16
	<i>Yucca filamentosa</i>			8			8
	<i>Rhus copallina</i>					8	8
	<i>Phoradendron flavescens</i>					7	7
Herbs	<i>Actinospermum angustifolium</i>	52	20	4			76
	<i>Monotropa uniflora</i>	2	6	55		11	74
	<i>Gelactia elliotii</i>	1	1	14	1	3	20
Totals		1036	818	1329	2675	1800	7658



will be covered by plants best suited to conserve the moisture supply. Or here, as everywhere, dry areas will be populated by xeric or semixerix forms. Observation of the condition existing in the scrub soil reveals the fact that the plants on the true scrub association grow in almost pure quartz sand, and there is no subsoil of a different character beneath; whereas the adjacent high pine association, for instance, covers a soil having a subsoil of yellow sand very near the surface. The two associations are delimited with extreme nicety. There is little or no overlapping, and the line of separation corresponds precisely with the line of meeting of the two types of sand referred



FIG. 2. Showing vegetation on scrub. Plat III.

to above. That is, the scrub vegetation ends where the white sand ends, and the high pine association begins where the yellow sand begins; and this line is definite and distinct. Several efforts have been made to explain this sharp limitation of the two types of growth. Nash (1895) thought that mutual antagonism between the groups of plants might account for the limitation of each. He called attention to a rather sparse growth of plants on a strip of ground between the scrub and high pine, and regarded it as a sort of neutral area where neither association could establish itself because of the antagonism of the other. Antagonism between individual species of

plants is, of course, well known, but that an entire community should array itself against a neighboring colony and maintain a neutral zone between them seems a bit fanciful. Whitney (1898) believed that the segregation is due to mere accident. Some forms, having preempted the ground, simply held it by squatter's rights. Revegetation of a burned scrub area, however, will show no admixture of high pine species, as apparently would occur if chance determined the new population. Harper ('29) points out that an abrupt change of soil from white to cream-colored is nearly always seen in passing from scrub to high pine. This suggests a rather close relationship between the phases of the soil and the vegetation growing upon it. So far as my own observations go, this sudden change of soil type is always to be observed where there is seen the very sharp delimitation of the plant associations. Animals are thought by Harper ('26) to be instrumental in mixing the soil on the high pine, and obviously they are very active in this connection, as shown by the numerous mounds thrown up by them. In the scrub almost no burrows are seen. Their absence may very well be due to the lack of cohesion of the white sand; it would be difficult for animals to keep the tunnels open. In the yellow soil, however, there is probably enough clay and silt to greatly increase the cohesion of the soil particles, and to make it possible for the animals to work successfully. I am disposed to believe that finally the solution of the riddle of plant distribution on scrub and high pine will be found to reside in the character of the two types of soil.

The transition from the scrub to a lake margin resembles in some respects the change from scrub to high pine, but there are many important differences. Some of the scrub species continue almost to the high water level of the lake, but in some cases, as stated elsewhere, their habit of growth is radically different near the water. Other forms stop rather suddenly at a considerable distance before the lake is reached, and new types take their places. The total population also changes radically here, as may be seen by reference to Table I. At the lower level, the surface soil is entirely different from that encountered on the typical scrub. Considerable organic matter has accumulated near the lake, and the upper 4 or 5 inches of soil has a dark gray color, as contrasted with the white sand of the more elevated areas. The deeper portion of the soil likewise changes as the lake margin is approached. Plats IV and V are like the high pine land in the matter of subsoil. At a depth of from 6 to 12 inches below the surface the yellow sandy subsoil is encountered. The scrubs are situated on what appear to be old sand dunes which were formed when this section was coastal—in the early geological history of the peninsula. Wherever the drift sand is of sufficient depth to prevent the plants roots from reaching a richer stratum of material beneath, only the scrub type of vegetation can become established. On the other hand, the yellow sand appears to be a more favorable material for the growth of such plants as require a large supply of water.

Considerable information as to the plant forms that will grow in the

scrub sand, if the water supply and other conditions are favorable, was gained by inspection of a sand pit which had been dug in the center of a relatively large scrub. This pit is about 300 yards in diameter, of an irregular outline, and ranges from 4 to 15 feet in depth. The deeper digging has reached the permanent water table, and there were a number of shallow pools at the bottom of these deeper excavations when the examination was made in November, 1930. The floor of the pit is uneven, and the sides expose the



FIG. 3. Showing vegetation near lake margin. Plat IV.

original soil structure to a depth of 15 feet. The removal of the sand took place in 1925-26, and sufficient time has elapsed for a new plant population to appear. In and at the edge of the pools are found such plants as the cat-tail (*Typha latifolia*), *Jussiaea suffruticosa* and *Proserpinaca pectinata*. Where the elevation is 2 or 3 feet above the water level many grasses have established themselves. Of these may be mentioned the sand bur (*Cenchrus echinatus*), Natal grass (*Tricholaena rosea*), Bermuda grass (*Cynodon dactylon*) and *Panicum nitidum*. A few willows (*Salix marginata*) are also found at the same elevations as the above grasses. Still higher (6 to 10 feet above the ponds) may be seen many herbaceous plants; pokeweed (*Phytolacca rigida*) and *Baccharis glomeruliflora* being conspicuous. Associated with these latter are such typical scrub plants as *Ceratiola ericoides*, *Garberia fruticosa*, and young seedlings of *Pinus clausa*. None of the typical scrub forms are found on the lower part of the pit floor. It is easy to believe that this distribution of types is determined by the water requirement of the

species involved. An alternative explanation may be that the deeper portions of soil possess more plant nutrients than the surface, and thus meet the requirements of plants which cannot grow in the surface soil for lack of proper nutrition; but, so far as I know, no such species grouping can be made on the basis of known nutritional requirements. The leaching of the surface has probably carried soluble material to lower levels where it has accumulated, thus depleting the surface soil while the lower portions have increased in plant food. Hardpan appears to have been formed in this way.

The vegetation now seen in the pit may possibly be the initial phase of a succession which will finally come to a typical scrub association or, what seems more likely, it may constitute a relatively permanent population. I am not inclined to believe that the typical scrub will ever occupy the floor of the pit, nor that the forms now present will entirely be replaced. No doubt there will be changes, some of the species now present, such as grasses and annuals, being eliminated as others come in, but there will hardly be a complete reversion to the original types which occupied the territory. The environment appears to be entirely suitable to many of the new kinds of plants, and the conditions are quite unlike those of the surface which was removed. Few of the plants in the pit are such as I have seen in a succession following a fire or on an abandoned field in a scrub area.

The sand pit also afforded a very good opportunity for the study of a cross section of a scrub soil to a depth of 15 or more feet. The surface 4 or 5 feet consists uniformly of the white sand phase of our deep sandy soils. In many places the white phase is uninterrupted from the surface to a dense, dark stratum of hardpan at a depth of 12 to 15 feet. At other points below the 4 or 5 foot surface layer the white phase is broken by the presence of masses of yellow sand varying in size from 1 to 5 feet in diameter. The face of a cut through where these yellow portions are found shows a distinctly mottled appearance. Wherever the roots of plants have reached down to these mottled areas great numbers of rootlets form a dense network in the yellow sand, while in the adjacent white portion only a few small roots are given off from the larger ones as they pass along. No doubt this large production of feeding roots is a response to a more favorable nutritional condition in the yellow sand as compared with the white areas. The pit did not extend to the border where the scrub meets the high pine land, but trenches dug from within the scrub to the high pine area showed the yellow sand lying over the white at their junction.

Tests have been made to determine the relative water-holding capacity of the two types of soil referred to above, and it was found that the yellow sand possesses, as indicated in Table II, from 6 to 7 per cent greater maximum moisture when saturated than does the white sand. This property would undoubtedly account for much of the difference between scrub or white sand associations and those growing on the yellow subsoil.

TABLE II. *Comparison of maximum water holding capacity of white sand and yellow sand soils*

Soil	No.	Water Held per cent	Average per cent
White.....	1	20.4	20.1
Sand (Scrub).....	2	19.8	
Yellow.....	1	26.6	26.5
Sand (High Pine).....	2	26.4	

A study of the water content of the soil on each of the plats gave the results indicated in Table III. The samples from which these results were secured were composites of 10 cores for the 6 inch depths and 5 cores for each of the deeper depth. The cores of samples were taken with the ordinary tube approved by the U. S. Bureau of Soils. The individual cores were taken 10 feet from each of the corners of the rectangle and in the center of the 100 × 100 foot squares. At all depths the water content is greater in Plats IV and V than in I, II or III, but, in some instances, very slightly so. There appears to be a region extending from the sixth to the twenty-fourth inch in which the moisture content of the soil is less than either at the surface or in depths below 24 inches. This is true for all but Plat II, and is clearly shown in the column of averages in Table III. These determinations were

TABLE III. *Moisture content of soil on the plats, in percent*
Plat Numbers

Depth of Sample	I	II	III	IV	V	Average
0 to 6 Inches.....	4.91	3.75	4.6	9.41	13.41	7.21
6 to 12 ".....	4.01	3.84	3.64	4.10	4.95	4.10
12 to 24 ".....	3.73	3.86	3.48	4.47	4.5	4.0
24 to 36 ".....	4.86	4.22	4.11	5.25	6.31	4.95
36 to 48 ".....	4.38	4.81	4.56	4.31	5.21	4.65
48 to 60 ".....	3.81	4.95	4.98	5.14	13.04	6.38
60 to 84 ".....	5.05	5.01	5.10	5.55	12.00	6.54

made in July during the Florida rainy season. The rains occur almost daily and usually last but for a short time, so that there is little fall during any 24 hour period. This would account for the greater surface water, as there would not be sufficient precipitation at any one time to penetrate the deeper layers, but enough to keep the surface well supplied. These figures show that the moisture content of all the plats is small as compared with the general run of soils, but is much greater than is found in scrub soils during our winter season. It must be considered, however, that such open soils will yield sufficient moisture for plant growth when they contain 2 per cent water or less, and it is this lower limit which determines whether a given species can exist on the scrub. In discussing the scrub vegetation, Harper ('14a) notes the close resemblance between scrub species and plants growing under arid conditions elsewhere, and again ('21) that scrub sand will support a low pine

vegetation at low elevations, where the water level is doubtless near the surface. That water is one of the chief controlling factors in determining the character of the scrub association is attested by the semixerix nature of the entire population. Each species shows some structural provision for the conservative use of water. *Pinus clausa* has fine, short leaves and close set scales on the younger twigs. *Ceratiola ericoides* has short needle-like, bristly leaves, and dense, dry, brittle wood. *Xolisma ferruginea* has thickly cutinized, densely tomentose, strongly revolute leaves, etc. The stomata are often obscured and small on some of the plants, and the leaves are greatly thickened and seldom exposed horizontally. The saw palmetto (*Screnoa serrulata*) shows an interesting variation in growth habit. On the true scrub, Plats I, II and III, the stems are completely underground, merely an upshoot of leaves being visible. At the lake rim the stems emerge from the ground and run freely along the surfaces, becoming several feet long, intermingling, and ascending at the ends, often to a height of 3 or 4 feet, forming an almost impenetrable tangle. As shown in figure 1, the elevation of the ground breaks rather abruptly at the beginning of Plat IV and continues steep to the lake. This corresponds rather well with the beginning of the change of species of plants. Water table tests show that the permanent level is practically the same as the surface level of the lake. On Plats I, II and III, therefore, the constant water is at least 21 feet below the surface, while on Plats IV and V it is from 0 to 21 feet. It is obvious that the plants on the upper areas can make no use of this deep supply of water, whereas on the lower half of Plat IV and all of V the roots may easily secure a supply from this source.

In the scrub sections there are many areas entirely free from vascular vegetation. These spots range from 3 to 12 or 15 feet in diameter. So far as the character of the soil or the exposure to sunlight are concerned, there is no manifest reason for the existence of such areas. If, however, one digs into the soil for a short distance the decaying roots of former occupants will often be found. The condition of the roots in many cases indicates that the shrubs which formerly occupied the land here have been dead for a considerable time. The parts of the plants which grew above ground have decayed long ago and their residue has been incorporated into the sand, indicating that the spots have remained bare since the former growth died, that is for several years. The lack of revegetation seems to result from the apparently extreme difficulty of seedling establishment in the scrub sand. The surface loses moisture so rapidly that very frequent and heavy rains would be required over a relatively long period, in order that the seeds might germinate and their seedlings send their roots into the ground sufficiently to withstand a subsequent drought. If, during a rainy season, there should occur a period of 3 or 4 days sunshine without rain, any seedlings which had recently developed would perish. Under the direct sunlight of mid-day,

when the relative humidity of the air is low, transpiration must often exceed absorption of water by the plantlet roots; hence, death will result from lack of water in the plant, although there is abundant moisture in the soil. Soil temperature alone is, no doubt, sufficient many times to cause death of large numbers of seedlings by protoplasmic coagulation. The scarcity of annuals on the scrub (only one of which appears in Table I, since the counts were made in January) may also be accounted for in the same way. In general, only those species which regularly produce great numbers of seeds, such as *Afzelia pectinata*, *Actinospermum angustifolium*, etc., are found on the scrub. Many of the scrub plants grow in clumps, as is the case with *Ceratiola ericoides* and *Xolisma ferruginea*, and the clumps become of considerable size. Now, if one of these communal groups should for any reason die, the space covered would quickly become bare, and the size of the group would determine the size of the denuded spot. Oxidation takes place rapidly in the porous sand. The dry organic matter is also easily blown from the bare areas. So, there is little accumulation of debris on the ground to form any kind of protection for seedlings, which otherwise might find favorable moisture conditions under leaves, small twigs, etc., shed from surrounding plants.

Some plants, such as *Geobalanus oblongifolius* and *Quercus. geminata*, which reproduce largely by underground runners, may finally populate the barren areas, but they are not particularly well suited to arid scrub conditions; hence, seldom make much progress in this territory.

It is well known that many kinds of plants require a soil of acid reaction for normal growth, or even for any growth at all. Such are the Vacciniaceae, Oxalidaceae, Polygonaceae, etc. Other families, of which Cassiaceae and Fabaceae are representatives, generally thrive best in alkaline soils. Still others, as Lamiaceae, Brassicaceae, and many others, appear rather indifferent to reactions within comparatively wide ranges. The recent introduction of accurate means of determining true acidity or alkalinity of soils has encouraged investigation of the part played by reaction on plant distribution, and results suggest the desirability of intensifying research in this field. Certain plant associations are no doubt largely determined by this ecological factor, and its influence may extend much further than we have been accustomed to believe. The reaction values secured on the survey here considered, and shows in Table IV, do not make evident any consistent variation corre-

TABLE IV. *Reaction of the soil in scrub and high pine, in pH*

Plat No.	0 to 6 Inches	6 to 24 Inches
I.....	4.83	4.63
II.....	4.83	4.56
III.....	5.27	4.92
IV.....	4.83	4.24
V.....	4.05	4.01
High Pine.....	4.76	5.09

sponding to the variation seen in the vegetation on the different plats. The results do not warrant any general conclusion concerning the influence of the pH on the populations of the areas designated in these studies.

On the whole, the results seem to justify the conclusion that water is an agent which has much to do with determining the character of the vegetation occupying the scrub sections. By this I do not mean to imply that all other recognized ecological factors are inoperative, but that the influence of no one is sufficiently evident to enable us to isolate its effect from the sum effect of all. Because of lack of facilities for making chemical analyses, no account of the chemical composition of the soil was taken; hence, this important item must be omitted from the discussion. Whitney (1898) and Harper ('21), using the same figures, appear to have reached somewhat opposite conclusions concerning the influence on vegetation of the chemical differences between scrub and the high pine soils.

SUMMARY

This appears to be the first published numerical survey of a Florida scrub, and shows a definite quantitative and qualitative difference between the vegetation on a typical scrub area and an adjacent lake margin. The transition is not so abrupt as that between a scrub and a high pine association. The lake shore vegetation is much more vigorous, and contains several species not found on the scrub. The scrub also has forms not growing at the lake margin.

Scrub plants are of the semixerix type, while those at the lake are mesic.

Near Windermere, Orange County, Florida, a rectangle 100 × 450 feet was laid off into 5 plats, 4 of which were rectangles containing 10,000 square feet each, and the 5th 5,000 square feet. These plats were further subdivided into rectangles containing 1,250 square feet each.

The scrub Plats I, II and III are on a terrain of white sand to a depth of at least 12 feet, while Plats IV and V consist of yellow sand at a short distance from the surface. Plat V bordered a lake.

The water content of the soils of Plats I, II and III was less than in IV and V. The determinations were made during the summer rainy season.

The water holding capacity of the yellow sand of Plats IV and V was found to be somewhat greater than that of the white sand of I, II and III.

Observations on a sand pit dug in a scrub showed that species of plants never found on the scrub will grow in scrub soil if the water supply is near the surface.

The conclusion is reached that water relations are major factors in determining the scrub association.

Determinations of the pH values did not reveal an appreciable difference between the soils of Plats I, II and III and the soils of IV and V, or of the high pine on yellow sand.

Animal activity in the soil was practically nil on all of the plats.

Revegetation of areas made bare by the death of former occupants is very slow, probably because of lack of water to support the seedlings. It may also be due to the inability of the young plants to absorb water as rapidly as it is lost by transpiration.

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ORIENTATION IN FRESH WATER FISHES

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The experiments of Lyon ('05*a*, '05*b*, '09) seem to show that rheotropism in fishes is a reaction which is brought about by a sense of relative motion. In a uniform current the fish heads upstream, not because it is under an actual current stimulus, but because it is attempting to maintain a constant visual image while the current is acting to carry the fish downstream. Garrey ('05) approached the problem from a different angle, but his results seem to dovetail with those of Lyon. Both of these experimenters were able to alter the orientation of the fishes by moving objects outside the aquarium. The fishes followed the moving objects in order to keep the same optical image. With a view to carrying forward these experiments and in an attempt to attach to them some ecological meaning, the following experiment was carried on.

STATEMENT OF THE PROBLEM

If the movement of a part of the immediate environment simulates the presence of a current in the still water of an aquarium, it would seem logical that in order to get the maximum reaction, two factors are important. First, both the sides and the bottom should be set in motion. Second, experiments should be made on fishes which are exposed to active currents in their natural habitats.

In the habitual surroundings of a fish, rarely does only one portion of the immediate environment move alone. The bottom of a stream does not move without the movement of the sides, and the sides do not move without the movement of the bottom. It is necessary, then, to bring about a condition where both the sides and bottom move as a unit, if we are to reproduce conditions which are relatively normal. Lyon has shown that a black and white striped cloth drawn under the bottom of a glass aquarium will cause orientation. Garrey has found that an object, preferably a bright one, when moved along the side of an aquarium will cause the fishes to change their positions. Steinman ('14) has worked along the line of the experiments of Lyon and Garrey, but his results are not conclusive. As a matter of fact his experiments bring in entirely new factors which are very confusing to the present theories of orientation through optical stimulation.

FISHES USED IN THE EXPERIMENT

Lyon's experiments were on *Fundulus* and sticklebacks; while Garrey tested only a school of sticklebacks. Neither *Fundulus* nor sticklebacks live

where there can be said to be a great deal of current. It seems truly remarkable that they react at all to the imitation current which is produced by the movement of a cloth along the bottom of an aquarium.

In the following experiment I have used fishes which are characteristic for the various ecological habitats of fresh water. The black-nosed dace (*Rhinichthys atronasus*) is found very near the head waters of small streams. It is constantly under the stimulus of rushing water, and seems to enjoy trying its strength against the current. The common shiner (*Notropis cornutus*) is found plentifully where the stream is relatively wide and the current not too strong. The darter (*Bolcosoma nigrum olmstedii*) is a bottom-living fish which is found usually in the quiet pools of the upper waters of a stream. The common sucker (*Castostomus commersonii*) can be found almost anywhere in the stream, but it is most numerous where the current is slow. The low position of the mouth of the sucker indicates the bottom-feeding habits of this fish. While the fresh water killifish (*Fundulus diaphinus*) seems to be able to adapt itself to any environment (Adams and Hankinson, '28), those which were used in this experiment were all taken from the small bays of a shallow lake. The sunfish (*Eupomotis gibbosus*) is a typical pond or lake fish. Even though it is sometimes found in the lower waters of a stream, it is seldom subject to the current of actively running water, and what lacustrine current does effect it is of entirely different type from the current of a stream.

All the fishes used in this experiment were taken from the lakes and streams of Saratoga County, New York.

APPARATUS USED IN THE EXPERIMENT

The apparatus used in the experiment was built around a glass aquarium, 9 inches wide by 14 inches long by 10 inches deep. The aquarium was supported by metal bars, so that a strip of cloth could be moved along under the bottom of it. In order to insulate the water in the aquarium from the vibrations caused by the movement of the cloth, pieces of sponge rubber were placed under the supports of the aquarium. Rollers were placed under the ends of the aquarium, and the strip of cloth was made to pass over the rollers in a continuous path (Fig. 1). Strips of buckram were attached to the strip of cloth in such a way that they were at right angles to the bottom and parallel to the sides of the aquarium. The buckram was so cut that it would pass around the rollers without bending. Both the cloth on the rollers and the buckram were painted with black stripes every third inch, making a black stripe one inch wide alternate with a white stripe two inches wide. The rollers, the cloth and the buckram were moved by a handle which was attached to the axle of one of the rollers. The entire apparatus was enclosed in beaver board so that the movement outside the experimental field could not be seen by the fish in the aquarium.

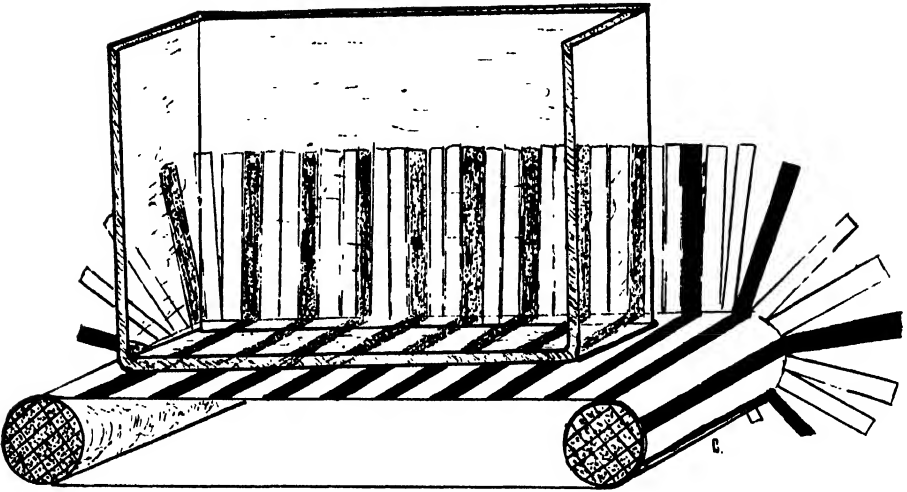


FIG. 1. Longitudinal section of the apparatus, showing the relation of the aquarium to the movable sides and bottom.

METHOD OF PERFORMING THE EXPERIMENT

On account of the limiting size of the aquarium, it was found best to use young fishes. They were brought into the laboratory and placed in aquaria until they had become accustomed to the temperature and confinement of the room. It was found best to put only one fish in the experimental aquarium at a time. The fish was placed in the aquarium of the experimental apparatus and allowed to stay over night. By this time it had recovered from the effects of handling and had become acclimated to the experimental environment. It was found that the fish needed this period of adjustment before it would react consistently. The artificial environment was then moved.

Either the movement of the sides or the movement of the bottom will cause the fish to orient, but the reaction is not as certain as when both the sides and bottom are moved together. Whether the movement of the sides or the movement of the bottom produces the stronger stimulation depends upon the position of the fish in relation to the sides or bottom. Under normal conditions, the bottom is the more important, although there is probably no sharp demarcation between the bottom and sides of the stream in the image which comes to the fish. Under experimental conditions, such as used in this experiment, the movement of the sides brings about the better reaction because the glass bottom of the aquarium reflects, to some extent, the movement of the sides so that it appears that both the bottom and the sides are moving.

RESULTS OF THE EXPERIMENT

All the black-nosed daces (*R. atronasus*) gave positive reactions to the movement of the sides and bottom, and definitely followed the stripes as they moved.

When the fish was lying quietly in the water and the cloth was moved slowly in the opposite direction from which the fish was headed, there was a slight movement backwards. But soon the fish would wheel and swim ahead in the same direction as the moving sides and bottom. By reversing the movement of the cloth it was possible to reverse the direction in which the fish was swimming. After the fish had been aroused by one reaction, the speed of the moving sides and bottom seemed to make little difference. As soon as the environment was moved, the fish would orient itself and swim in the direction of the movement of the sides and bottom. Upon the change of the swimming direction, the black-nosed dace would swim rapidly until either it reached the end of the aquarium or was reversed by the reversal of the moving surroundings. In no case did the fish swim faster than the movement of the sides and bottom.

The common shiner (*N. cornutus*) showed the reaction to the slowly moving sides and bottom better than any other fish tested. By moving the cloth slowly, the fish could be brought to any place in the aquarium. These fishes seem to be able to swim backwards easily, for it was possible to cause them to swim tail first the whole length of the aquarium. In this manoeuvre the caudal fin is brought far to one side and the more powerful stroke is toward the head. The pectoral fins play a part in this movement. They are wide spread and beat in short strokes.

When the sides and bottom of the aquarium were moved quickly, the shiner gave a reaction which could not be produced in any other fishes tested. Instead of accompanying the movement of the stripes on the surroundings, it definitely swam against the movement. One shiner which was particularly sensitive to any type of stimulation, always swam in the opposite direction from the moving sides and bottom. Shiners which have been kept in the aquarium for a long time also show this 'negative' reaction even when the movement is slow.

The darter (*B. nigrum*) was absolutely apathetic. Not the slightest action could be elicited by the movement of the sides and bottom. It would lie on the bottom of the aquarium and take no heed of the moving environment.

Lyon suggests that the tactile sensation of being in contact with a solid body, such as the bottom, may nullify the optical sensation of movement. By suspending the fish on a silk thread which was attached to a floating cork, it was possible to lift the fish from the bottom of the aquarium and remove the contact stimulus. Even under these conditions it was impossible to obtain definite results with the darter. As soon as the sides and bottom were

moved, the fish would attempt to swim to the bottom, but in no case was there any attempt at orientation.

The common sucker (*C. commersonii*) gave positive results, but the time of the reaction was not as fast as that of the black-nosed dace or even the shiner. The sucker swam along the aquarium with its mouth on the bottom, and when the cloth was moved slowly took up a position with its head pointing in the direction of the moving stripes. Upon the reversal of the movement, the fish lazily reversed its position.

The killifish (*F. diaphinus*) was not as consistent in its reaction as had been expected. While there can be no doubt that there is orientation, it is not as certain as in stream fishes. Sometimes the reaction was fast and sure; at other times it was slow and hesitant.

The sunfish (*E. gibbosus*) was the most interesting fish tested. Its slow and deliberate motions could be watched easily. It would lie quietly in the water and slowly turn to orient itself as the sides and bottom moved past. There was not an attempt to swim along with the movement of the stripes as in the other fishes which gave positive reactions. As the movement of the cloth was reversed, a few strokes of its pectoral fins would reverse the position of the fish and there the reaction would stop.

CONCLUSIONS DRAWN FROM THE EXPERIMENT

It would surely be a misnomer to place these experiments under the heading of rheotropism or rheotaxis, because there was no current. As a matter of fact everything was done to do away with any movement of the water. Under normal conditions orientation and rheotropism are probably inseparable. The first part of a reaction to current is to become oriented. The stimulus of the moving environment is undoubtedly an optical one. The fish sees the environment rushing past and takes up a position which will best permit it to react favorably.

It would seem logical that a fish which lives in fast water would react to the orienting stimulus more quickly than the fish which lives in slow water. There is no doubt that the stream fishes do react more quickly and more definitely than the lake fishes which were tested in this experiment. Also there seems to be a relationship between the speed of the current which is the natural habitat of the stream fish and the speed of its reaction. But the difference in the reaction time to the optical stimulation will not, I believe, entirely account for the difference in the position of these several fishes in their places in the stream or in the lake. At least it will not do for bottom living fishes nor for bottom feeding fishes.

The 'negative' reaction of the shiner (*N. cornutus*) to the fast moving environment is strictly against the theories of optical stimulation in orientation. At this time it seems impossible to explain it. This reaction might be used as an answer to Steinman ('13) when he says, "Anderer seits ist es

unmöglich, durch die Lyonsch Hypothese das aufwärtswandern zahlreicher Fische zu erklären, die zum Teil sehr bedeutende Strecken zurucklegen. Die rein optische Orientierung kann nur für abwärtsstrebende oder 'an Ort' schwimmende Tiere in Betracht kommen." However it must be explained before we can accept the optical stimulation theory as the whole story of orientation in rheotropism.

Optical stimulation undoubtedly plays a part in rheotropism under certain conditions, but there are other factors, as important or more important, which must be taken into consideration before we can solve the whole problem from an ecological point of view.

Under the conditions of this experiment, the following conclusions may be drawn to show the effect of optical stimulation on the orientation of certain fresh water fishes.

1. In the black-nosed dace, the common shiner, the common sucker, the fresh water killifish, and the sunfish the movement of a striped cloth along the bottom and sides of a glass aquarium causes orientation.
2. The stream fishes, the black-nosed dace, the common shiner, and the common sucker reacted more definitely than the lake fishes, the killifish and the sunfish.
3. The shiner, under certain conditions reacted 'negatively.'
4. The bottom-living fish, the darter, did not react to the optical stimulation.
5. The present theories of orientation solely through optical stimulation will not wholly explain the problem of longitudinal ecological succession in streams.

SUMMARY

The optical stimulus caused by the movement of a striped cloth along the bottom and sides of a glass aquarium resulted in orientation of certain fresh water fishes. The fishes turned so that they headed in the same direction in which the environment was moving. There seems to be a proportionate relationship between the speed of the fish's reaction to the optical stimulus and the speed of the water which is the natural habitat of the fish.

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INSECT INJURY OF BLUE GRASS IN RELATION TO THE ENVIRONMENT ¹

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That the relative amount of injury from larvae of the June beetle sustained by permanent pastures of southern Wisconsin is directly correlated with environmental factors, has been definitely established by further investigations carried on during 1930 in continuation of the work begun in 1927. Experimental data in this paper show that following the introduction of equal numbers of larvae in variously controlled cultures of blue grass (*Poa pratensis* L.) the injury was much more severe when conditions of growth were not favorable for this grass. In addition, numerous counts of grub populations in permanent blue grass pastures have shown a much greater abundance of larvae where the sod development of grasses has been retarded by deficiencies in limiting factors of growth. Such data will be published in a later paper.

The injury due to the white grub (*Phyllophaga* spp.) has become exceedingly serious in permanent grasslands and cornfields in southern Wisconsin (Fig. 1). That which occurred in 1927 and 1928 recurred with much greater severity in 1929 and 1930. As is well known, most of the species of the white grub have a life cycle of 3 years, of which approximately two thirds is spent in the larval stage, so that during all or a part of each year these insects feed on grass roots and rhizomes. The adults (June beetles) however, feed on the leaves of trees, such as *Quercus*, *Tilia*, et al. In parts of southern Wisconsin the beetles were so abundant in their flight of May and June, 1929, that oak trees were largely denuded of their foliage. The small grubs which hatched during the summer months of 1929 from the eggs laid by these beetles were so numerous that by autumn large areas of grass sod were completely severed from the soil. In the fall of 1930, after the larvae had been in the soil for more than a year, the blue grass and other grasses in large pastures of 100 acres and more (as well as smaller pastures) largely failed to recover after abundant rainfall. Thus the grub problem has become exceedingly acute as a factor in pasture management in Wisconsin, and an investigation from the viewpoint of both the insect and the grass was urgent.

This discussion will aim to set forth rather definite results in which the

¹ Contributions from the Departments of Agronomy and Economic Entomology, Wisconsin Agricultural Experiment Station, Madison, Wisconsin. Published with the approval of the Director.

intensity of grub injury of blue grass (as measured by the thickness, rate of growth and productivity of this grass) is affected by factors of its internal and external environments. A survey during 1927 and 1928 of the old permanent pastures of southwestern Wisconsin by Graber² had shown sharp



FIG. 1. This sod of an old blue grass pasture was lifted with ease, exposing larvae of the June beetle at the rate of approximately 400,000 per acre. The severance of root growth and the consumption of rhizomes has been almost complete, intensifying the effects of drought to the point of complete mortality of large areas of grass. With abundant and well distributed rainfall, however, the grass might have survived and recovered from such extreme injury. Especially would this be true if the soil were fertile and if the grass had received grazing treatments conducive to the accumulation of an abundance of organic food reserves. Such conditions help to develop a thick sod which tends to reduce the injury and also the infestations.

contrasts in the extent of grub injury in adjacent areas. In general, wherever the root and rhizome development of blue grass (the dominant species),

² Graber, L. F., Penalties of low food reserves in pasture grasses. *Jour. Am. Soc. Agron.*, 21: 29-33, Jan. 1929.

and of other grasses, was retarded by deficient fertility, or by deficient organic food reserves due to previous close premature grazing or by thin and dry soils due to hillside outcroppings of limestone or flint, there, the injury was made very evident by a diminution in the plant population and in the rate of growth and by a rapid secondary succession of ragweeds (*Ambrosia*), mullein (*Verbascum*) and other undesirable plants. In 1929 and 1930, many of the better pastures which escaped severe injury in 1927 and 1928 were badly hurt by extreme numbers of larvae whose injury was greatly intensified by the summer's drought.

This paper will describe an effort essentially to reproduce with controlled cultures of grass, the environmental conditions of the field where sharp differences in the grub injury of adjoining pastures occurred. Contrasts in the general factors of the field environment representing optimum and deficient conditions of the organic food supply, of fertility and of moisture were provided for blue grass grown in box cultures. Two such experiments were set up, and are designated as Experiments I and II. The latter was much more extensive and complete, while the former was in the nature of a preliminary trial.

EXPERIMENT I

Methods

Sixteen boxes, approximately 1 square foot in surface area and 10 inches in depth, were filled and packed with a mixture of one half rich loam soil and one half pure quartz sand. Eight of these boxes of soil were given surface applications of ammonium phosphate (containing 16.5 per cent N. and 20 per cent available P_2O_5) at the rate of 1,000 pounds per acre and potassium nitrate (containing 38.6 per cent K and 14 per cent N) at the rate of 500 pounds per acre. The remaining cultures were not fertilized until later.

On February 18, 1930, the boxes were placed in the greenhouse and seeded with blue grass. An optimum moisture content was maintained so that by April 28, 1930, a thick even growth of blue grass occurred in each culture, with blades averaging approximately 5 inches in length for the grass growing on the unfertilized soil and fully an inch longer where the soil was fertilized. On May 8, 1930, all cultures were fertilized with ammonium sulphate at the rate of 440 pounds per acre.

The top growth was removed in all cultures on April 28 by cutting the grass about three-fourths of an inch above the soil surface. (Table I.) Subsequently, 4 cultures of the heavily fertilized grass and 4 of the grass less heavily fertilized were cut about three-fourths of an inch above the soil surface on May 14 and 31, June 13 and 28, July 7 and 14, August 19 and September 4. These will be known as the cultures with low reserves. The remaining cultures were cut only on May 31 and July 7 at a height of $2\frac{1}{2}$ inches, and on September 4 at a height of $\frac{3}{4}$ inch. These will be known

as high reserve cultures. On September 9, the last cutting date, all grass was cut very closely leaving a stubble not more than $\frac{1}{8}$ inch in length. The differences in fertility as expressed by the growth of plants were not large, despite the heavy applications of fertilizer to some of the cultures prior to seeding. The contrasts in organic food reserves, however, were made very pronounced by the different cutting treatments employed. All cultures were given moisture to provide for optimum growth.

As will be noted in Table I, white grubs (from eggs laid in 1929) were introduced in each culture of grass at the rate of 17 per square foot on May 31, 8 per square foot on June 25 and 13 per square foot on July 30. After June 11 all cultures of grass were removed from the greenhouse to a lawn where temperatures were much lower during the summer months than under glass. The last date of cutting the top growth was September 9, and at this time the subterranean growth of the grass (including small remnants of stems and leaves not readily cut at the soil surface) was removed, washed, dried and weighed and the surviving grubs counted. (Table I).

Relation of Reserve Foods to Grub Injury

In this experiment, cultures of grass were developed with high and low reserves by means of frequent and infrequent cuttings and by variations in the height of cutting. Half of the cultures of high and low reserve grasses were heavily fertilized, and the remaining cultures were fertilized less abundantly. On August 19 nearly all the grass of the low reserve cultures was killed by the grubs, whereas the cultures of high reserve grass showed relatively slight injury. On September 4 the high reserve grasses were cut $\frac{3}{4}$ inch from the surface soil, and yet in 4 days they produced an excellent recovery as indicated by the yields on September 9 (Table I).

The principal condition limiting growth of the grasses in this experiment was the situation with reference to organic food reserves. The soil was fertile at the outset, and the comparative responses of the grasses with complete fertilization and fertilization with nitrogen only were not prominent. The cutting treatments, however, were so severe in half of the cultures that the reserves were lowered and root and rhizome growths were curtailed, and no doubt the regenerative capacity of this grass was lowered. Since white grubs feed on such growths; the injury was intensified to the point of death of practically all the plants with low reserves by August 19 (Fig. 2). The high reserve grass survived the injury from the introduction of equal numbers of grubs, and was still in a productive condition at the close of the experiment. The comparative amounts of top growth removed on September 4 and 9, and the subterranean growth removed on September 9 (Table I), are definite evidence of the extreme differences in the amount of grub injury from approximately equal numbers of grubs feeding on grasses with high and low reserves.

INSECT INJURY OF BLUE GRASS

July, 1931

TABLE I. *Experiment I. Relation of organic food reserves and fertilization to the productivity of blue grass undergoing injury from equal numbers of the larvae of the June beetle.*
Cultures of grass were seeded February 18, 1930

Treatment of grass and soil		No. of cul- tures of blue grass	Average dry weight in grams of top growth of blue grass per square foot. 1930.												Number of larvae introduced			Dry † weight subter- anean growth	Number of larvae
Reserves	Fertili- za- tion		Before larvae were introduced				After larvae were introduced												
			4/28	5/14	5/31	Total	6/13	6/28	7/7	7/14	8/19	9/4	9/9†	5/31					
High	Abundant complete	4	29.4		7.8*	37.2			5.6*			56.5	17.0	17	8	13	24.0	20	
	Nitrogen only	4	24.3		6.9*	31.2			3.5*			37.5	22.7	17	8	13	24.6	25.5	
Low	Abundant complete	4	29.1	7.0	1.4	37.5	1.4	1.4	4.9	3.4	.5	.1	0.0	17	8	13	.8	7.5	
	Nitrogen only	4	22.8	8.9	1.6	33.3	4.0	4.3	9.0	5.0	1.3	.1	.1	17	8	13	.8	17.5	

* Cut 2½ inches above soil surface.

† Includes a small amount of top growth—about ⅛ inch which remained after cutting.

‡ Cut ⅛ inch above soil surface.



FIG. 2. Experiment I. Only blue grass with high food reserves survived the injury from white grubs which had been introduced in equal numbers in the above cultures. Although favorable conditions of moisture and fertility were provided throughout the experiment, and an even sward of grass prevailed in each culture prior to the introduction of the larvae, the grass with low food reserves was completely destroyed.

The grass with high reserves maintained a larger population of grubs at the close of the experiment (Table I), and had such an abundance of roots and rhizomes which the grubs were not able to consume that a relatively vigorous top growth prevailed throughout the entire period of the trial. In the boxes of low reserve grass, where nearly all the underground growth was consumed, a smaller population of larvae was found at the termination of the experiment, due perhaps to an insufficient food supply causing death or migration.

EXPERIMENT II.

Methods

Forty eight boxes made of sheet iron, each with a top area of $1/40,000$ of an acre and 10 inches in depth were partially filled with carefully sifted Miami silt loam soil collected at the University Hill Farm at Madison, Wisconsin. After 24 of these boxes had been filled to within 3 inches of the top, the following fertilization was applied:

Superphosphate (20 per cent P_2O_5)1,000 pounds per acre.
 Potassium nitrate (39 per cent K, 14 per cent N)1,000 pounds per acre.
 Calcium carbonate2,000 pounds per acre.

On this fertilizer there were added 2 inches of sifted soil and then $3/4$ inch of rich garden loam soil which had previously received a generous application of composted manure. The remaining 24 boxes were filled with soil in the same manner but without fertilization. The object of applying the fertilizers at a 3 inch depth in the soil was to avoid an immediate contact with the grubs which were to be introduced later.

Blue grass seed was sown on May 3, 1930, at the rate of 150 pounds per acre, and then covered with a layer of $1/4$ inch of garden loam soil. Within

40 days the grass had developed a uniform sod in each of the boxes of fertilized soil, and the leaf growth attained a length of from 5 to 6 inches. The grass in the boxes of unfertilized soil also developed uniform sods but had only from 3 to 4 inches of leaf growth. Moisture was applied uniformly to all cultures and at such a rate as to promote optimum growth until June 12, 1930. After this date optimum water relations were continued in only half of the fertilized and half of the unfertilized cultures. The remaining cultures were maintained on a deficient moisture basis. No effort was made to weigh the amount of moisture applied to any of these cultures, but the condition of grass was used as a criterion for determining the water applications. With the minus moisture cultures the grass was kept in a state of retarded growth without attempting to approach a minimum moisture status. With the plus moisture cultures an effort was made to maintain the grass in an optimum state of growth.

Between June 17 and July 22, 1930, the grass was cut so as to develop a relative condition of high reserves in part of the cultures and low reserves in the remainder. The low reserve condition was obtained by cutting the grass within about $\frac{3}{4}$ inch of the soil surface on June 17, 26 and July 7. The high reserve condition was maintained by clipping the grass $2\frac{1}{2}$ inches above the soil surface on June 17 and July 7. On July 22, just one week before the introduction of white grubs in the cultures, all the grass was cut at a uniform height of $\frac{3}{4}$ inch from the soil surface.

It should be stated here that all the cultures were kept in the greenhouse until June 11 when they were moved to a frame structure which was completely screened to keep out all but the smaller insects. The boxes of grass were placed on a soil level about 6 inches below that outside the frame. The upper portions of the iron boxes were greased with a mixture of sugar, lard and an ant poison which was very successful in discouraging infestations of ants in the cultures.

On July 29, 1930, some 1,500 live grubs (from eggs laid in 1929) were collected and late in the afternoon 47 were placed in each of the 16 cultures of high reserve grass and 45 were placed in each of the 16 cultures of low reserve grass. This left 16 cultures of grass without grubs, consisting of 2 check cultures for each of the 8 cultural treatments applied (Table II). The grubs were protected from sunlight by shading until they had buried themselves in the soil. Any grubs which had failed to "dig in" by the following morning, were replaced with more active individuals. On August 10 ammonium phosphate (16 per cent N and 20 per cent P_2O_5) was applied on the surface of the sods at the rate of 200 pounds per acre, and only to those cultures which had been fertilized before seeding. It is probable that this fertilization had no influence on the capacity of the grubs to survive in the cultures. The relatively low rate of mortality (Table II) as demonstrated by the numbers of surviving grubs on August 28 and September 9,

TABLE II. Experiment II. *Relation of organic food reserves and fertilization to the relative productivity of blue grass grown under conditions of optimum and deficient moisture, and with and without the introduction of white grubs.*
Grass sown in soil cultures on May 3, 1930. Grubs introduced July 29, 1930.

Treatment of grass and soil			No. of cultures	No. of grubs introduced	Ave. no. of live grubs in each culture	Average dry weight in grams of growth removed from cultures of grass—1930															
						Before introduction of larvae					After introduction of larvae on 7/29										
						Top growth					Top Growth				Subterranean Growth						
						8/28	9/9	6/17	6/26	7/7	7/22	Total	8/28	9/9	Total	% Loss	8/28	9/9	% Loss		
Optimum	High*	Fertilization	2	47	33		5.3		6.5	13.2	25.0	54.6				11.7					
			2	47		32	6.5		6.3	15.2	28.0	33.2	24.4	57.6	23			10.9	74		
			2	None	None	None	4.0		8.0	15.7	27.7	44.3	30.9	75.2				42.0			
			2	47	36.5		2.8		3.0	9.3	15.1	41.9					21.8				
			2	47		32	2.3		4.0	10.5	16.8	18.7	25.2	43.9	7			33.8	54		
	Low †	Fertilization	2	None	None	None	5.2		5.4	11.1	21.7	21.5	25.5	47.0				73.5			
			2	45	30		13.6	11.5	10.6	6.6	42.3	14.0					8.8				
			2	45		30	15.5	12.1	13.7	3.8	45.1	8.3	7.3	15.6	53			8.0	39		
			2	None	None	None	12.5	9.5	13.2	4.0	39.2	18.6	13.8	32.4				14.5			
			2	45	32		9.6	8.4	8.3	4.0	30.3	5.1					3.3				
	Fertilization	2	45		31	10.5	9.0	11.7	3.8	35.0	2.6	1.0	3.6	77			2.3	90			
		2	None	None	None	4.8	21.7	8.5	2.2	37.2	7.4	8.4	15.8				22.8				

* High organic food reserves were maintained by cutting the grass $2\frac{1}{2}$ inches above the soil surface on June 17 and July 7, and $\frac{3}{4}$ inch on July 22.

† Low organic food reserves resulted with cutting the grass $\frac{3}{4}$ inch above the soil surface on June 17 and 26, July 7 and 22.

TABLE II (Continued)

Treatment of grass and soil		No. of cultures	No. of grubs introduced	Ave. no. of live grubs in each culture	Average dry weight in grams of growth removed from cultures of grass—1930														
					Before introduction of larvae										After introduction of larvae on 7/29				
					Top growth					Top Growth					Subterranean Growth				
Moisture	Organic reserves	Fertilization	7/29	8/28	9/9	6/17	6/26	7/7	7/22	Total	8/28	9/9	Total	% Loss	8/28	9/9	% Loss		
Deficient	High *	Abundant	2	47		5.1		4.9	10.2	20.2	43.2					8.6			
			2	47	36	3.6		6.3	6.8	16.7	17.3	20.8	38.1	33		8.3	71		
			2	None	None	4.1		5.5	13.3	22.9	27.1	29.5	56.6			29.0			
		2	47	35	1.6		3.1	7.1	11.8	35.0					10.6				
		2	47		4.3		3.6	5.5	13.4	16.4	10.8	27.2	37		7.2	77			
		2	None	None	2.8		2.3	9.3	14.4	22.5	21.0	43.5			31.8				
	Low †	Abundant	2	45	34.5	12.8	10.8	6.5	7.2	37.3	8.0					6.8			
			2	45		16.4	9.0	10.2	6.2	41.8	2.9	2.9	5.8	70		4.1	78		
			2	None	None	12.6	10.4	8.9	4.0	35.9	7.0	12.3	19.3			18.5			
		2	45	35.5	8.2	9.5	7.8	4.0	29.5	3.3					2.3				
		2	45		11.1	10.1	8.1	4.4	33.7	1.1	.9	2.0	88		4.4	76			
		2	None	None	8.5	7.0	11.1	3.2	29.8	6.6	10.7	17.3			22.5				

is indicative of the hardness of this insect in its larval state. On August 28, the grass was removed from 16 boxes representing each of the 8 environmental conditions of the experiment. The top and subterranean growth were separated, washed, dried and weighed. The remaining cultures of grass were also cut on August 28, but at a height of $\frac{3}{4}$ inch from the surface of the soil. The grass in these cultures was cut very close on September 9, when the root and rhizome growth was removed, dried and weighed (Table II).

General Discussion of Methods

By reference to Table II, the 8 general combinations of the optimum and deficient conditions of moisture, fertility and reserves is made clear. In trying to develop these situations an attempt was made to avoid the intensification of one limiting factor of growth to the point where the others would be "over-shadowed" with relation to the growth of the grass. In developing low organic reserves the cutting treatments were not severe, but in relation to the high reserve treatment a fair contrast prevailed.

The differences in soil fertility were not exceedingly pronounced despite the heavy applications of fertilizers to some of the cultures. In normal seasons the Miami silt loam soil used in all cultures is sufficiently fertile to produce 50 bushels of oats an acre and a fair crop of clover and alfalfa without liming or fertilization. While far from satisfying the exacting requirements of blue grass for its optimum growth, the soil was average in its general fertility—being neither very poor nor very rich.

The differences in the moisture relations of the various cultures were not so extreme as to mar the expression of the other factors of growth which were being studied. It is very evident that any one of the 3 general limiting factors of growth studied in this experiment could have been so intensified as to almost completely obliterate an expression of the other 2. This was true, in part at least, with the contrast in reserve foods of the cultures of blue grass used in Experiment I.

INFLUENCE OF ENVIRONMENT ON THE GROWTH OF BLUE GRASS INFESTED WITH WHITE GRUBS

In Experiment II, the grubs were intentionally introduced at a rate (1,880,000 grubs per acre in cultures of high reserve blue grass and 1,800,000 in the low reserve cultures) from 4 to 6 times as abundant as they are generally found in severely infested grass sods in the field. This was done to hasten the injury so that results might be obtained before cold weather would destroy the insects. Nine days after their introduction in the grass cultures unmistakable evidence of injury was present in all the low reserve grass. There was not only a retardation in the growth of the grass in comparison with the check cultures (in which no grubs had been introduced)

but the roots and rhizomes of the low reserve grass had been severed in patches and the plants, with about $\frac{1}{2}$ inch of the clinging soil, could be lifted with great ease. At this time (August 7), and on alternate days thereafter, a numerical estimate was placed on the amount of injury in each culture. This was ascertained by a comparison of the plant population and rate of growth of check cultures (without grubs) with the corresponding cultures which had identical treatment save for the introduced grubs. The results of these observational determinations are shown graphically in Figures 3 and 4. As indicated in Table II, the cultures representing 8 different environmental conditions are first grouped into those given optimum and those receiving deficient moisture. Each of these is divided into cultures of grass with high and low reserves which in turn are subdivided into those receiving abundant fertilization and those given no fertilization.

The injury sustained by the grass from the white grubs was very much intensified in cultures grown with relatively slight deficiencies of moisture. This was expected. White grubs feed largely on the horizontal plane of rhizome growth leaving but a thin layer of soil on which the remaining roots must largely depend for sustaining top growth. Obviously, the absorptive capacity of such grass was much impaired. A comparison of the curves in figures 3 and 4 reveals the marked contrast in the amount of injury which occurred in cultures of grass with optimum and deficient moisture. Those cultures of grass which had been cut in a manner to provide for an abundance of organic foods were injured the least, particularly when fertilized.

With optimum moisture (Fig. 4) the cultures of grass growing under the most unfavorable environment with reference to reserves and fertility were generally injured most rapidly. Fertilization of the low reserve grass greatly reduced the injury but with high reserves this was only true from August 7 to 27. On the contrary, the grub injury appeared more severe in the fertilized cultures of high reserve grass from August 29 to September 8. An explanation of this condition may be found in a study of the amount of root and rhizome growth in check cultures (Fig. 5). In every fertilized culture of grass, whether grown with optimum or deficient moisture, the amount of subterranean development was less than that of the corresponding unfertilized grass. Apparently, heavy nitrogenous fertilization of blue grass tends to stimulate vegetative growth and limit subterranean development. Especially was this true where the accumulations of old top growth were so abundant as to exclude sunlight from the new leaves. The new growth, being etiolated for a considerable period, was established largely from previously stored foods and at the expense of root and rhizome growth. Such etiolated growth is often killed by sudden exposure to sunlight after cutting, thus delaying the recovery³ of the grass and, at least temporarily, retarding its regenerative activity. This was very obvious in the centers of the cultures

³ Graber, L. F., Food reserves in relation to other factors limiting the growth of grasses. *Plant Physiology*, 6: 31-71, 1931.

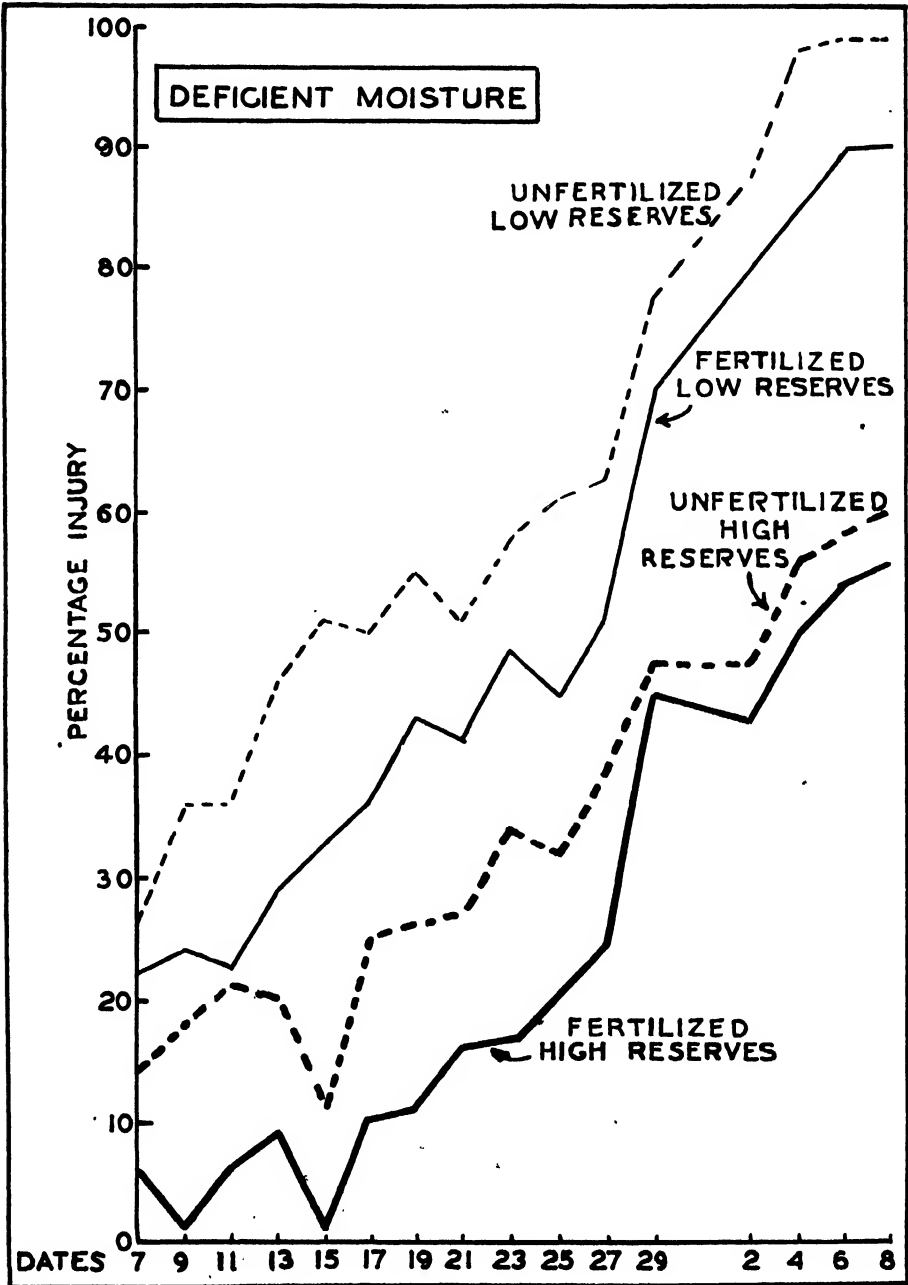


FIG. 3. Experiment II. Deficient moisture intensifies the grub injury of blue grass especially where fertility and organic foods are limited. This is graphically portrayed for the period of August 7 to September 8, during which the percentages of injury were ascertained by estimates based on the rate of growth and the plant populations of grass with and without infestations of grubs. Compare figures 3 and 4.

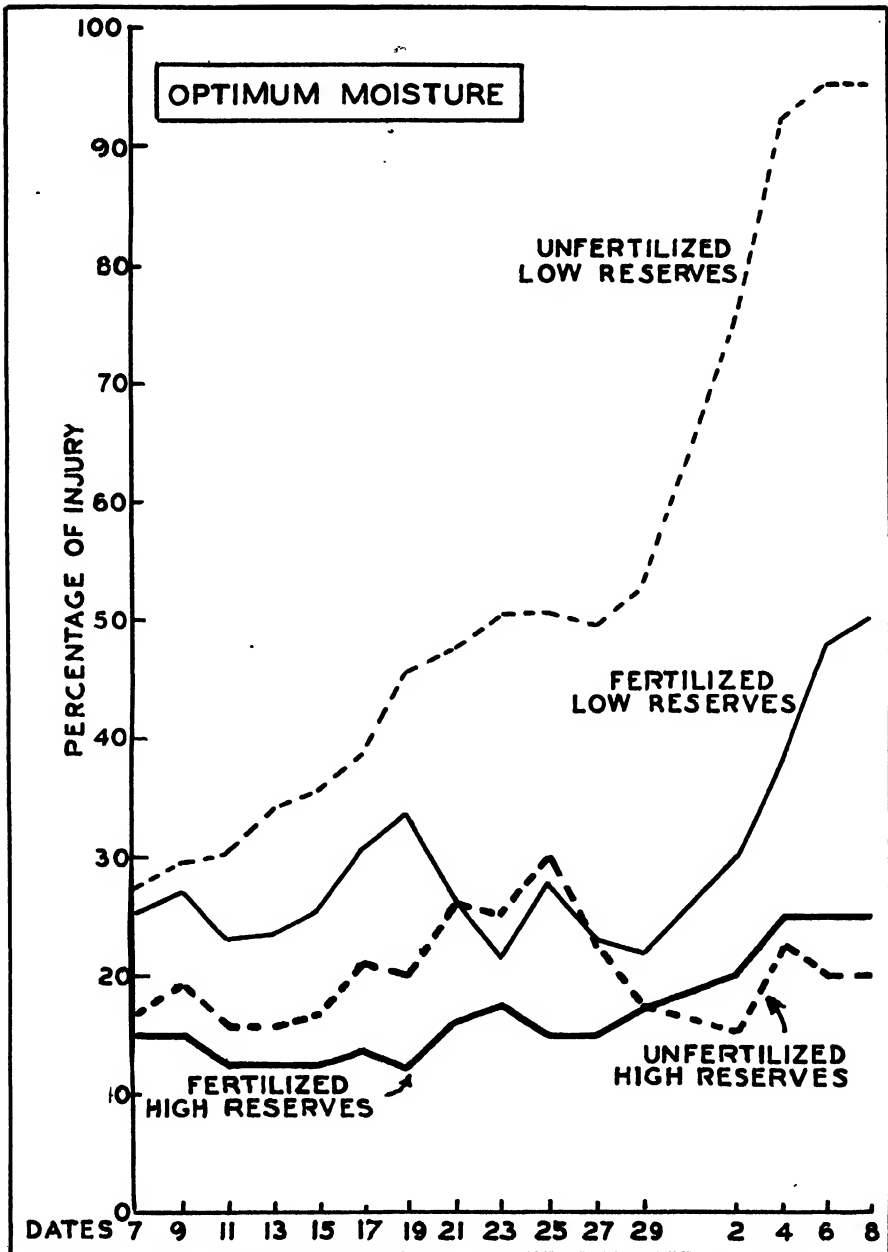


FIG. 4. Experiment II. Although optimum conditions of moisture were provided, the injury from the larvae of the June beetle to blue grass increased most rapidly with the unfertilized blue grass low in reserves. The degree of injury was ascertained by estimates based on comparison of the rate of growth and plant populations in cultures of blue grass with and without infestations of white grubs. Blue grass with high reserves and optimum moisture showed relatively little injury, whether fertilized or not. See figure 3.

of all high reserve grass, and particularly when such cultures were provided with fertilization and optimum moisture. The root and rhizome growth was also much less, and the sods much thinner in the centers of these cultures than at the borders where more light reached all leaf growth and particularly the basal portions of the grass. It therefore appears quite

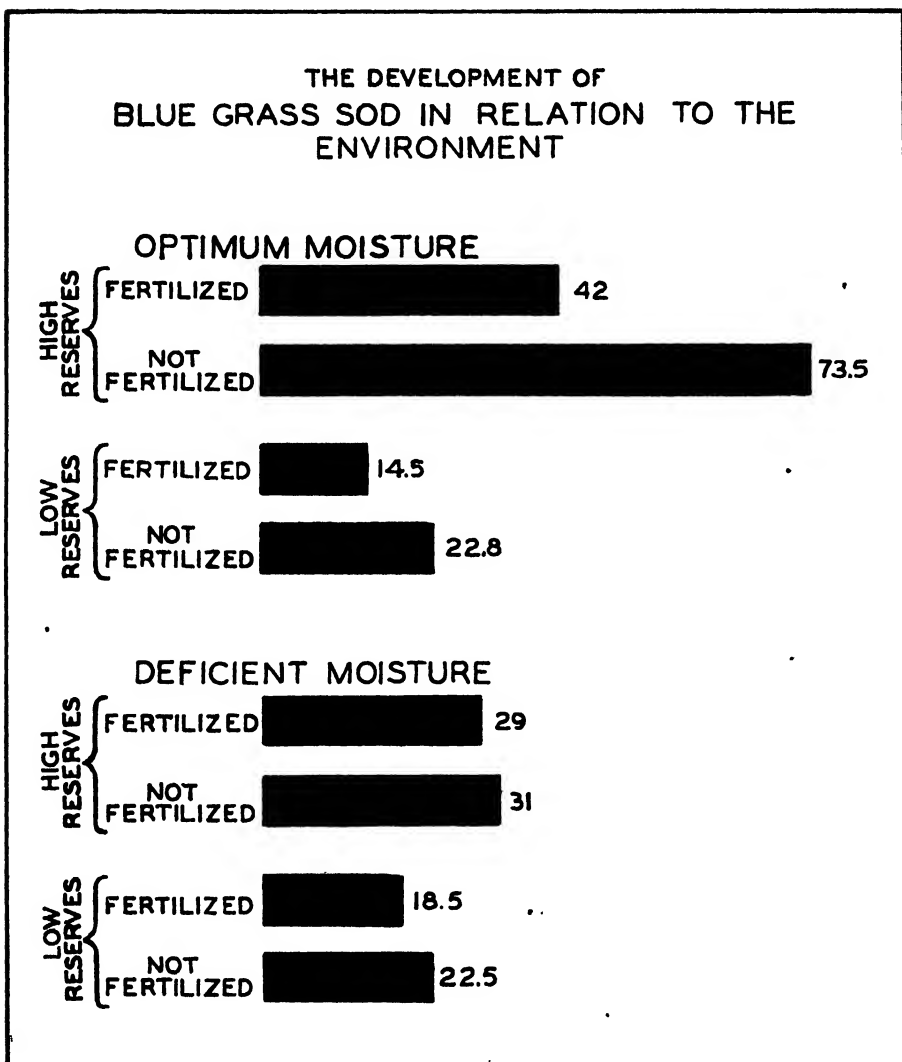


FIG. 5. Experiment II. The dry weight in grams of root and rhizome growth in all the check cultures of bluegrass (in which no grubs were introduced) is shown graphically from data presented in Table II. Organic food reserves and moisture are the two conditions having the greatest influence on sod development in this experiment. Abundant nitrogenous fertilization reduced the amount of subterranean growth during the 128 days subsequent to seeding on May 3, 1930.

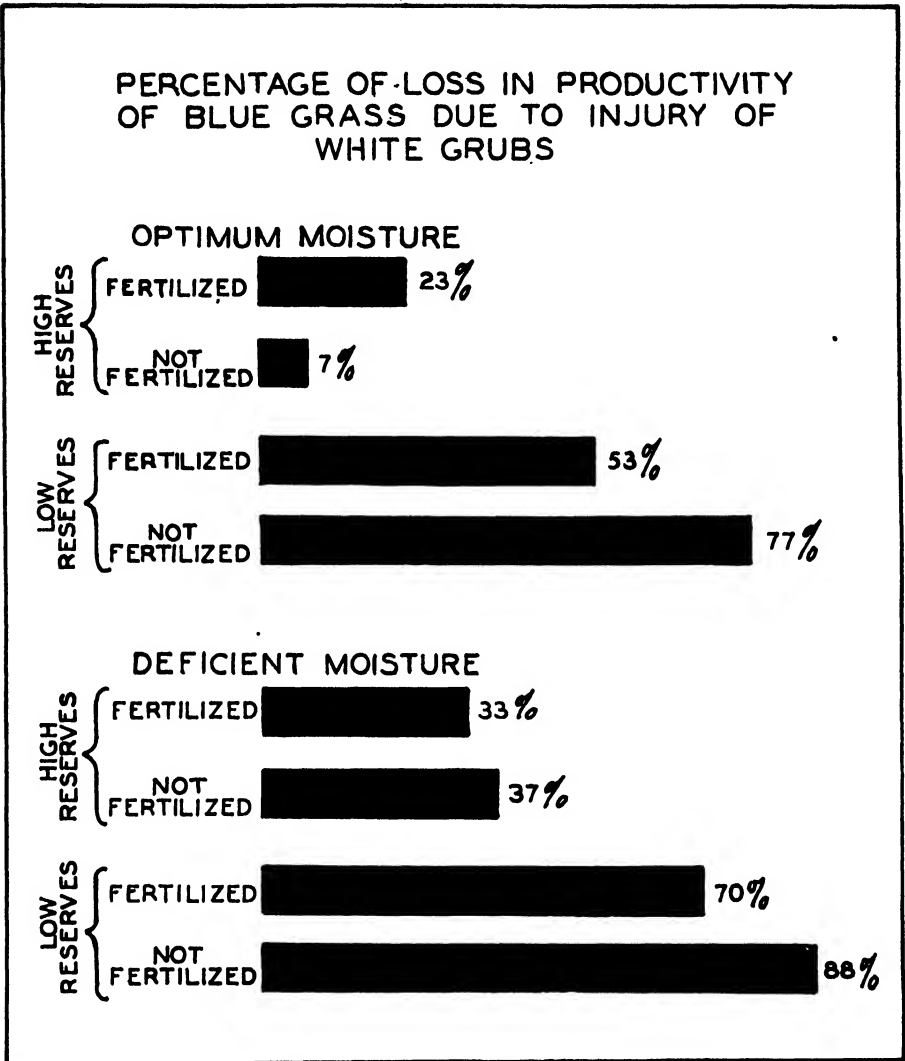


FIG. 6. Experiment II. The loss in productivity of top growth of blue grass due to injury of white grubs was ascertained by comparing the amount of top growth removed on August 28 and September 9 from cultures of blue grass in which larvae had been and had not been introduced on July 29, 1930. (Table II.)

evident from the data presented in Table II and portrayed graphically in figures 5 and 6, that the degree of injury sustained by blue grass from the white grubs was related not only to the amounts of subterranean growth the plants were able to produce but also to their regenerative activity during the feeding period of the insect. It is also probable that blue grass plants approaching maturity utilize more water and exert a heavier draft on the

moisture content of the soil than those with frequent defoliations. When this and other pasture grasses are cut off by the insect from the normal subterranean supplies of moisture and nutrients during stages of major water needs, they would seem to have less opportunity for regeneration and survival in times of drought. Such considerations are speculative but they may account, in part, for occasional field observations where, with dry weather and under uniform soil conditions and apparently uniform populations of white grubs, greater injury occurred when grasses were allowed to mature than when given moderate grazing or cutting treatments.

In all cultures of Experiment II, grass with the high reserve treatment developed by far the greatest amount of root and rhizome growth, and such grass suffered the least injury from the grubs. On the other hand, heavy nitrogenous fertilization lowered the amount of subterranean growth as compared with corresponding cultures of unfertilized grass, particularly where excessive accumulations of top growth occurred from optimum moisture and from high reserves. With the exception of such grass, the injury from white grubs (Fig. 6) was decreased rather than increased with fertilization. This is effectively explained by the activation of the subterranean buds with abundant nitrogen. Such activity may not express itself in producing the greatest total quantity of root and rhizome growth but rather in developing the greatest capacity to regenerate new growth when the old has been injured by the insect. When regeneration was not complicated by the inhibitions from abundant accumulations of top growth, fertilization aided the grass in "out-growing" the injury it sustained from the insect, even though the amount of subterranean growth was lessened.

The percentages of loss in productivity of top growth caused by larvae of the white grub are more specific measures of the relative amount of injury sustained by the bluegrass. Such data (Table II, Fig. 6) were obtained by a comparison of the total yields (on August 28 and September 9) of top growth from control cultures of this grass with those infested with grubs. The results are a remarkable confirmation of the observational estimates on the relative amount of injury from August 7 to September 8 as shown in figures 3 and 4. Again the evidence is clear that losses in productivity due to grubs were greatly intensified by deficiencies of moisture principally in the surface layer of the soil and by limited organic food reserves in the plants (Fig. 7). Fertilization tended to reduce the amount of injury in all cases except under conditions of high reserves and optimum moisture (Fig. 8). As previously explained, an abundant top growth of blue grass resulting from heavy nitrogenous fertilization may have inhibiting effects on subterranean growth and on recovery which would tend to amplify the injury from the grubs.

The presence of unremoved old and new growth in the cultures of blue grass when the grubs were introduced, has diminished rather than increased the percentages of loss in productivity due to insect injury. The stubble

(old growth) which remained after cutting on July 22, and the new growth between July 22 and July 29, had been produced without the retarding influence of insect injury, and yet they were a considerable part of the ultimate yields of top growth.



FIG. 7. Experiment II. With deficient moisture and without fertilization the injury occasioned by white grubs has been greatly intensified by previous cutting treatments which have prevented the accumulation of organic foods. This is effectively illustrated by the amount of recovery in the growth of the above cultures of blue grass during a period of 24 days after cutting on July 22, 1930. Larvae of white grubs were introduced in the two cultures at center on July 29, 1930.

The productivity of top growth (Table II) in control cultures as well as in those infested with grubs is very closely correlated with the environmental conditions. Moisture, organic food reserves, and fertilization have affected

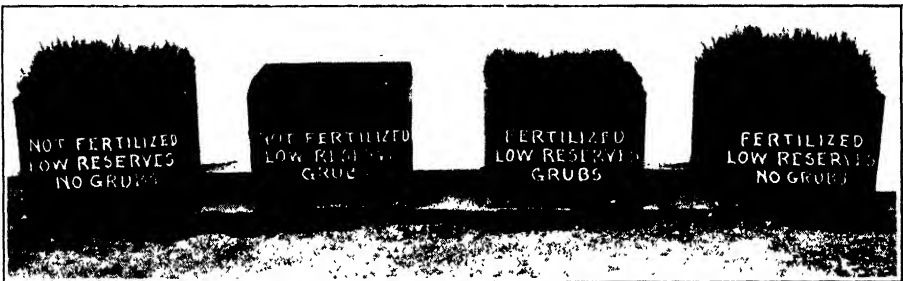


FIG. 8. Experiment II. The fertility of the surface layer of soil is important in the maintenance of grass the roots and rhizomes of which have been largely severed by white grubs. This is shown by the relative amount of recovery in the growth of blue grass (above) under favorable conditions of moisture and for a period of 24 days after the last cutting on July 22, 1930. Larvae were introduced in the two cultures in center on July 29, 1930.

the yields prominently both before and after the introduction of grubs (Fig. 9). Probably the surface application of ammonium phosphate on August 10 was more effective in aiding regeneration of new growth of blue grass after a considerable portion of the roots and rhizomes had been severed or con-

sumed by the grubs than the more abundant and much deeper fertilization which was applied to the soil before seeding. The yields (Table II) of top growth of blue grass on August 28 do not appear consistent because two cultures from each treatment were given a final cutting at the soil surface while the remaining cultures (2 infested with grubs and 2 controls) were cut $\frac{3}{4}$ inch above the soil surface. The latter cultures were not cut closely or finally until September 9.

The amount of root and rhizome growth (including small remnants of top growth not removed in the last cutting) was ascertained in both grub

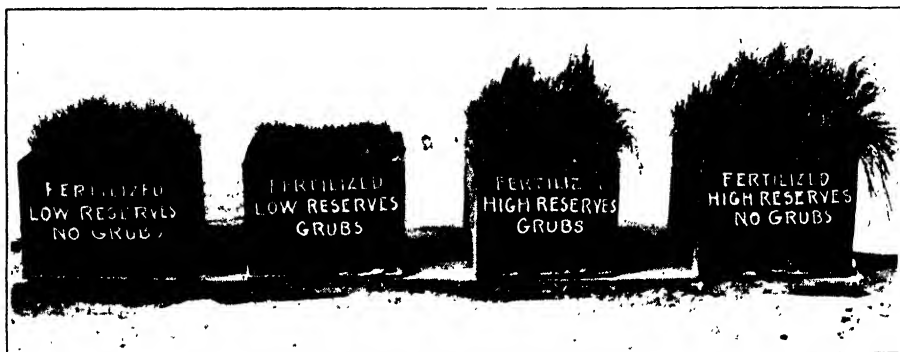


FIG. 9. Experiment II. The amount of injury from white grubs (two center cultures) was much greater with blue grass having low organic food reserves even though favorable conditions of moisture and fertility were provided. The above growths of grass occurred during the period of July 22 to August 15, 1930. Larvae of white grubs were introduced in the center cultures on July 29. (Table II.)

infested and controlled cultures of blue grass, and is expressed in Table II. Since there are many possibilities of error in making quantitative determinations of subterranean growth of blue grass, the interpretation of such data needs careful consideration. It is exceedingly difficult to separate the soil particles from the fibrous roots without some loss of such roots in the washing process. This also holds true when more complete separation is made by partial drying of the sod. Furthermore, in this experiment the sod included remnants of the top growth which could not be conveniently removed exactly at the transition region of top and underground growth. Errors resulting from such factors were significant, principally, with the determinations of small amounts of subterranean growth such as obtained in the blue grass with low reserves. Although the percentages of loss in root and rhizome growth occasioned by the grubs could not be determined as accurately as they were with the top growth, such calculations were made and are given in Table II. They indicate that from 39 to 90 per cent of the root and rhizome growth was consumed by the grubs in the cultures receiving optimum moisture, and from 71 to 78 per cent in cultures grown with deficient moisture.

Determinations of the number of surviving larvae in cultures of grass on August 28 and September 9 indicate a surprising uniformity. The mortality of the grubs (introduced July 29) averaged only 27 per cent and varied from 23 to 32 per cent. Although slightly more numerous in the cultures of high reserve grass with deficient moisture, a much more widely varying mortality was expected.

The capacity of blue grass to ultimately survive or recover from injury by the insect, as was demonstrated in Experiment I, might have been used as another criterion of the relative amount of injury sustained by the cultures of grass used in Experiment II. The continuation of the trial, however, was not feasible on account of the lack of facilities for conducting the experiment under conditions of abundant autumnal rainfall, frosts and generally lower temperatures. Consequently, the introduction of a large number



FIG. 10. In narrow ravines where the soil was favored with moisture and fertility, the grub-injured blue grass recovered with autumnal rainfall. This was in sharp contrast to the conditions of the adjacent slopes where the sods were killed by a combination of drought, infertility and larger numbers of white grubs.

of white grubs on July 29, 1930, was considered desirable to intensify and hasten the injury of the grass and thus provide satisfactory data before the results would be complicated by such climatic variations. The recovery with autumn rainfall, in ravines, as contrasted with adjacent slopes, is shown in figure 10.

SUMMARY

The injury to blue grass resulting from the consumption of subterranean growth by white grubs (*Phyllophaga* spp.) was greatly intensified by all unfavorable conditions of the external and internal environments of the plant.

This situation was indicated by field surveys in which the relative extent of the injury to pastures from white grubs had been correlated with deficiencies in fertility of the soil, in the organic food reserves of the plants, in moisture and in combinations of such general factors influencing growth. To gain more specific evidence, however, such conditions of the field were reproduced in cultures by definite fertilization and cutting treatments, and by regulation of the moisture supply. The introduction and maintenance of approximately equal numbers of white grubs in a part of such cultures, and the utilization of the remainder as controls, made possible a study of the relation which the external and internal environments bear to the degree of grub injury sustained by blue grass. This was measured, in part, by observational estimates based on plant populations and comparative rates of growth of infested and control cultures of blue grass grown under a wide range of environmental conditions. These results were corroborated by quantitative determinations of top growth in which the percentages of loss in productivity due to grub injury were ascertained from specific yields of the grub infested cultures and the controls. With blue grass grown under conditions of optimum moisture, such reductions in productivity varied from 7 to 23 per cent when cultures of this grass had been cut to maintain an abundance of organic foods, and from 53 to 77 per cent when such foods were less abundant. Likewise, the white grubs reduced the yields of top growth of blue grass grown with deficient moisture from 33 to 37 per cent when the grass was in a state of high reserves, and from 70 to 88 per cent when the reserves were low. Liberal fertilization tended to reduce the injury in all cases except where accumulations of leaf growth inhibited the subterranean development and the regenerative capacity of the grass to a marked degree. Thus it appears evident that the injury from white grubs is lessened when conditions favor the quantitative development of subterranean growth of blue grass, and especially when such factors of the environment augment the regenerative activity of the grass during the feeding period of the insect. That the environment of the plant is significant in relation to insect injury is made manifest.

TYPES OF HUMUS LAYER IN THE FORESTS OF NORTHEASTERN UNITED STATES

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The aim of the present paper is an orientation on the natural types of humus layer in the forests of northeastern United States. Observations on the distribution of the different types and their characteristic vegetation are reported, and a classification based on morphological characteristics is attempted. The field studies are supplemented by nitrification tests, determinations of pH, loss on ignition, lime content, and some mechanical soil analyses. Most of the field work reported on has been done by the authors in cooperation. The field work has been carried out mainly in New York State and New England; but some observations in Pennsylvania and the Lake States are also included.

The term *humus layer* is used for the top layer of the soil, owing its characteristic features largely to its content of organic matter (Hesselman, '26, pp. 207, 516), no matter whether this content is high or low and whether the humus is an *Auflagehumus* (Vater, '28, p. 132) lying on top of the mineral soil, or is incorporated in the soil proper. The term proposed seems to cover this conception better than does *humus cover*, the latter term suggesting a cover of unincorporated organic matter. *Humus* is taken to represent the organic residues in all stages of evident decomposition, and its accumulating transformation products, but not the litter, *i.e.*, the fresh debris, not yet attacked to any extent by the soil organisms, and lying loosely or more or less compressed on the surface.

The central question involved is that of a workable classification. This problem, international in scope, has hardly been finally solved thus far for any region, and it is probably unnecessary to stress that the proposals made in the present paper should be regarded as tentative. Even so, they might be of some value as a first systematic attempt to apply P. E. Müller's principles to American conditions and as a contribution from America to the international discussion on an urgent question of classification.

A brief historical review will serve as an introduction to the problem.

Historical Review

C. EMEIS AND P. E. MÜLLER

The German forester Emeis seems to have been the first to state clearly some of the striking differences between various types of humus formation

occurring in the forest. He distinguished three classes of forest humus, the first of which corresponds to the true mull (cf. below) and the other two representing different kinds of raw humus. These two classes will be mentioned again later. Here attention will only be drawn to a remarkable statement in Emeis' book with regard to Class 1. He says that in this Class 1, but not in the other two, the nitrogen "can be expected largely as nitric acid." As is well known, it was later doubted for a long time that any nitrification occurred in forest soils, so Boussingault's old positive findings had to be rediscovered by Weis ('08) as late as 1908. Moreover, later extensive researches by Hesselman and others have led to a general conclusion about the distribution of nitrification in forest soils which is not very far from Emeis' flat statement in 1875.

More than 10 years before Emeis' work, a contribution (von Post, 1862), now classic, on natural types of organic deposits had appeared. Von Post dealt principally with lacustrine formations, of which he distinguished two types, different in properties and mode of formation. These types, *dy* and *gyttja*, are still currently used by Swedish quaternary geologists and limnologists, and not only the conceptions but even the terms have been taken up to some extent internationally. Von Post also attempted to classify the non-aquatic organic deposits, but here he was not as fortunate. It was not until the work was taken up and carried further by the Dane, P. E. Müller, that von Post's ideas and procedure proved a success also in this field.

Müller was probably the first to look upon the humus layer in the forest as a natural biological unit, and, by careful field observation, microscopical examination and some chemical tests, he was able to characterize two main types of humus layer and their biological and silvical properties in a way which has substantially stood the test of the time. The modern school of forest soil research, represented by Hesselman and others, builds altogether upon the foundations laid by Müller, and his statements and points of view are still, after more than 50 years, in most cases quite up-to-date. His silvical applications today form the backbone of Danish forestry thought.

On the other hand, outside of Scandinavia, Müller's work, although quoted very frequently in the literature, often appears to be little known in detail. It is not rare, for instance, to find his rather widely adopted term mull used in a sense differing from the conception of its author, in spite of the fact that Müller's work has been published in one German (Müller, 1887) and one French (Müller, 1889) edition besides the original Danish text (Müller, 1878, 1884).

RAMANN AND HIS FOLLOWERS

It is difficult to account fully for the inadequate attention given to P. E. Müller's work on humus types in Ramann's *Bodenkunde*, which, as the standard textbook in the young science of forest soils, has had a dominating influence. In the last edition Ramann ('11) thought that it was "in line

with P. E. Müller's intentions " to let the word "mull" stand for that part of the soil which consists of animal excrements. In parenthesis, he then gives the expression "mull soil" as meaning any forest soil with a friable, crumbly structure. None of these definitions covers exactly Müller's conception, which is a certain *natural type of humus layer*.¹ The main progress performed by Müller is discarded by narrowing the sense of his term *mull*, as Ramann did, to designate merely a constituent of the natural deposit, which in fact occurs, in varying amounts, in most types of humus, if not in all of them.

Unfortunately, Ramann's attitude has been followed more or less by many other authors. Recently it has been most curiously applied by Albert ('29, p. 105) who defines mull as humus which has been brought into the soil in solution, or has originated there (contrasted with "Moder," which has been brought in mechanically). According to this definition, a bad humus podsol could be richer in "mull" than many good mull soils. Curiously enough, even Scandinavian authors, although adhering in a general way to Müller's views, seem to have been contaminated by these tendencies. The result is the use of the word "mull" in a very illogical way to stand either for the whole natural deposit or merely for its humus content (Ekström, '29, Frosterus and Tamm, '29, parts of the same committee report). Bornebusch ('30a) has been aware of this inconsistency and tried to avoid it, unfortunately by changing Müller's nomenclature, in current use in Denmark and elsewhere, to fit the sterile Ramann scheme.

THE REGIONALISTS' VIEW

As P. E. Müller was the first definitely to prove, soil formation processes stand directly under the influence of the humus layer. The type of profile formed is strongly, although not strictly, correlated to the humus type.

Nevertheless, the humus layer has been somewhat neglected in pure soil science, perhaps due to the overwhelming influence of the climatic concept, and seems often to be looked upon merely as the tool of the climate in soil formation, its efficiency being regarded as practically exclusively determined by the climate, be it directly or indirectly. A characteristic statement is the following by Glinka ('14, p. 7): "At present, the importance of the climate can be proven also in another way. As already mentioned, the leaching is a result not only of atmospheric but also of biological influences. Inasmuch as it seemed clear that the decomposition of the organic debris on the soil

¹ It is unfortunate that a serious error of interpretation concerning this point has slipped into the French translation of Müller's work where it is erroneously stated (p. 91) that the underlying stratum is just as high in humus as the mull. This mistake is particularly unfortunate inasmuch as the French edition seems to be more accessible than either the German or the original Danish. The error mentioned has been perpetuated by Russell ('27) and from there has been taken over by Toumey ('28), and possibly by others.

surface and in the soil is affected mainly by lower organisms, which occur in enormous numbers in the water, the air and the earth's crust, the question arose about the conditions under which these organisms live and work. Experiments showed that the intensity and character of their action is determined in first line by temperature and moisture." Glinka goes on to explain how a slow decomposition will form an excess of humus, which will be more oxidized and saturated with bases when the decomposition is hindered by lack of moisture, less oxidized and saturated when too high a humidity is the cause of the slow decomposition.

These appear to be purely theoretical deductions, and do not altogether agree with observations. P. E. Müller and others have shown the type of humus layer to be dependent not only on climate, but also on such things as the character of the vegetation, which can vary because different plants grow in the same climate. A poorly oxidized and unsaturated raw humus, may form as a result of lack of moisture as well as of excess moisture. In general, the same biological equilibrium may appear under rather different combinations of factors, and, in the causative complex, edaphic factors, such as lime and ground water, often seem to be just as important or more so than climatic ones. This is very well illustrated by the distribution of the true mull type of humus layer (see below).

It would almost seem as if already the Russian scheme for designating the different soil horizons, which has now become international, reflected a certain neglect of the humus layer. As far as podsolized forest soils are concerned, it is certainly inappropriate to include the humus layer and the leached layer below it in the same main horizon A.

There are indications, however, that even regional soil scientists may feel the need of distinguishing humus types. As one particularly remarkable instance Marbut's ('28) "scheme for the differentiation of soils into mapping groups on a uniform basis for all countries" may be cited. In this scheme, the sub-groups within the main group I, comprising all the humid soils of the world, are characterized, among other ways, by the nature of the humus layer.

Earlier Schemes of Classification

P. E. MÜLLER

Müller distinguished two main types of humus layer called *mull* (Danish spelling *Muld*)² and *mor* (Danish *Mor* or *Maar*). The most typical representative of the former group is the earthworm mull, a porous, typically loose, friable mass with a crumby structure, and consisting of an intimate mixture

² This is probably the same word as the English *mould* or *mold*, and is by many authors translated in this way. Inasmuch as there are two English words mould or mold with very different meanings, one of which in a particularly unfortunate way leads the thought to an abundance of fungus growth, it would seem desirable to adopt the word *mull* also into English to cover Müller's view, as has been done by a number of authors; in this country by Toumey, '28, and Fisher, '28.

of humus with mineral soil. The organic matter content of the mixture is usually low, in Denmark below 10 per cent. The deposit is inhabited by large earthworms, such as *Lumbricus terrestris*, and supports a rich vegetation of geophytes (Müller, 1887, 1894).

The other, the *mor* group, comprises matted humus layers usually very high in organic matter and lying like a carpet on top of the mineral soil. The deposit is more or less tough or compact, or both, not porous and friable like the mull. The large earthworm species are missing.³ The vegetation is strikingly different from that on the mull type, not only in the absence of the typical mull plants but also in the occurrence, often even abundance of plants (Ericaceae, mosses, etc.) absent or rare on the mull.

Between the typical representatives of these two groups there are, of course, transitional phases. Müller mentioned some such forms, and particularly one which he called *insect mull*, or *mull-like mor*. It was found locally in small depressions, etc., in areas mostly covered with *mor*, forming a deposit up to 4 or 6 inches thick consisting mostly of organic matter, but loose and friable, looking like a mass of fine, dark brown saw-dust. There was a considerable root concentration in the surface, but no dense root mat. The patches with this kind of humus layer were associated with raspberry bushes and particularly thrifty young beech, and showed a varied ground flora. No vegetation could be indicated as characteristic for this type, however, because most of the plants of the beech forest could occur. The name *insect mull* for the type was suggested by Müller because he found a great many chitin remains in the deposit, and also because the sawdust-like granules gave the impression of being insect excrements. This is not the case, however, with an evidently closely related form (Müller, '10, p. 210, footnote), *Alpenhumus*, to which Ebermayer (1888) drew attention in a review of Müller's studies.

LATER PROPOSALS

The above foundations were laid by Müller over 50 years ago, and soon showed their practical value. Nevertheless, comparatively little has been done, even in his own country, to continue the work in his spirit. Striking proof was seen when one of the authors visited Denmark last summer, mainly to ascertain what Müller referred to by his *insect mull*, and was unable to get this information from the best available sources. The less pronounced mull forms, particularly, have received little attention except for the *Alpenhumus* or *Alpenmoder*, monographed by Leiningen ('08-'09) and recently treated by Tschermak ('30). After all, this is not as astonishing as it might seem. In Danish, south Swedish and French hardwood forests, Müller's two main categories have been sufficient for practical purposes. In the

³ Müller did not find any earthworms in the typical *mor*, but according to recent studies by Bornebusch ('30a) small forms are present, and the difference in this respect between the two groups is that only the mull harbours the *large* earthworm species. Müller attributed a dominating importance to the latter.

softwood forests of Germany, northern Scandinavia and Finland, the mull is so rare that the silvical interest centers on the variations to be found within the other main type. Thus it is natural that most of the later proposals have dealt with the question of a suitable subdivision of the *mor* group.

Instead of the already existing term *raw humus* (Rohhumus), Müller chose in the German edition of his studies the unfortunate term *peat* (Torf) for his *mor* group. Ramann (1893, p. 232) felt the need of distinguishing the heavy, tough, more extreme and inert forms of the group from the thinner and looser ones which decompose in a few years on a cut-over area, and adopted for the former Müller's *peat*, only changed to *dry peat* (Trockentorf), while retaining the old term *raw humus* for the latter lighter forms. This division in two groups has since been used to some extent, but does not seem ever to have been universally adopted. Outside Germany, raw humus has become largely synonymous with Müller's *mor*, and in Germany *Rohhumus* and *Trockentorf* have been used alternately at different times and by different authors to designate the whole group or its more pronounced members. Ramann himself abandoned his own scheme in the second edition of his textbook ('05) where he designated the whole group as Rohhumus with the remark: "Müller denotes it as Trockentorf" (p. 160). In the third edition ('11) he again changed, apparently influenced by the recommendation given to the term Trockentorf by a congress of forest experiment stations in Stuttgart in 1906,⁴ and accepted *Trockentorf* instead of *Rohhumus*, although with some hesitation (p. 195). Recently *Trockentorf* seems to be growing increasingly unpopular, even in Germany, and it has been proposed to change it to *Auflagetorf*, this term to be used either instead of (Vater, '28, p. 133) or together with (Albert, '29, p. 104) *Rohhumus*.

This is not the whole story, however, about the evolution of the classification and terminology of humus forms in Germany. Parallel to the juggling with the words *Rohhumus* and *Trockentorf* goes the development of a new category and the tendency to classify *constituents* of the humus layer rather than the humus layer as a whole. Both trends seem to have been inaugurated by Ramann.

In the second edition of the *Bodenkunde*, where Müller's division in two main groups, mull and raw humus, was followed (Ramann, '05, pp. 156-157), he brings together, in another connection (pp. 176-178), the *Alpenhumus* and several other non-aquatic humus deposits under the name of *Moorerden*.⁵ These were characterized as humus soils consisting of peat material so strongly decomposed (*zersetzten*) that no debris with discernable plant structure remain, and forming a loose mass, mostly with granular structure. In

⁴ Trockentorf was agreed on again in 1908 by the Association of German Forest Experiment Stations (Vater, '28, p. 133).

⁵ In the first edition, *Moor* was used only for deposits formed under water, as a synonym to von Post's *dy*; in the second edition, both the *dy* and the *gyttja* of von Post are included under *Schlamm*, which in the first edition was synonymous with the latter only.

the third edition (Ramann, '11), this group reappears under the name of *Moder* in a classification of humus rather than of the humus layer, now elevated to the same rank as *Mull* and *Torf*, and with the definition: "Dis-integrated organic remains with organized (?) structure, the plant structure of which is discernible microscopically, but not or hardly macroscopically."⁶

Since that time, *Moder* seems to have become firmly established as a term in Germany, but the definition has continued to fluctuate. Vater ('28, p. 133) takes it as that part of the unincorporated humus which comes right under the litter and consists of "products of plant remains, still in loose layering, but more or less humified."⁷ Krauss' ('30) proposal of "*Moder-schicht*" as a German equivalent to Hesselman's *F-layer* (see below) seems to be quite in line with Vater's definition. On the other hand, Albert's ('29, p. 104) definition of *Moder* as "a loose, soil-like mass of homogeneous appearance, macroscopically structureless" seems to be much nearer to the older definitions by Ramann.

The situation is further confused by the tendency, persisting in Germany since Ramann, to prefer a classification of the humic material to a classification of the humus layer. Ramann expressed himself very clearly in this direction in 1911 (p. 195): "One could, for instance, make the description this way: 'Beech raw humus of compact Trockentorf, below which 3 cm. compact *Moder*'; or 'Raw humus in pine forest, 10 cm. loose Trockentorf, below which 10 cm. *Moder*'; or 'Raw humus forming a compact finely fibrous *Moder* layer 2-3 cm. etc.'" In this way, "one would escape all difficulties," Ramann says. This might have been true if the same words had not been used both to designate the types of humus layer and to distinguish certain strata in the natural deposit or certain stages of decomposition. The tendency has been the other way, however, and at present not one of the terms discussed is not used in Germany in a double or triple sense. It is not easy to see how an intolerable confusion could be avoided with such practice.

Like Ramann in 1893, Hesselman in Sweden has felt the need of distinguishing certain better forms of the raw humus group from the rest. He has been particularly concerned with a raw-humus-like but thin, rather loose and little coherent *Hylocomium*-humus, characteristic of productive moss-rich mixed softwoods in central Sweden. In its lower part, it is somewhat mixed with mineral soil, and upon the opening of the stand, it readily enters into a nitrifying stage. Hesselman ('17b, p. 935) makes it parallel with the German *Moder*, but it would also seem to correspond rather closely to Ramann's raw humus of 1893. In 1917, Hesselman made his form a special variety of the raw humus group, and designated it tentatively as *mossmylla* (about =

⁶ "Als *Moder* kann man alle zerkleinerten und zerteilten organischen Reste mit organisierter Struktur bezeichnen, deren Pflanzenstruktur makroskopisch nicht oder nur undeutlich erkennbar ist, aber unter dem Mikroskop hervortritt" (p. 172).

⁷ "Die mittlere Stufe besteht aus Stoffen, welche aus Pflanzenabfällen hervorgegangen sind und noch lose lagern, aber mehr oder minder humifiziert sind. Sie wird mit '*Moder*' bezeichnet."

moss humus), a good and telling word. In 1926, however, he unfortunately followed Sernander's example⁸ in expropriating Müller's word *mor*, only spelling it *mår*, and applied this term to his *Hylocomium*-humus, raising it to the same rank as null and raw humus, and putting it as a third type between these two. If it had not been for Sernander and Hesselman, there would at least have been no confusion around the term *mor*.

Before proceeding to the most recent suggestions as to the classification of types of humus, it is desirable to stop and consider the proposals made for distinguishing the different layers or strata within the humus layer. Ramann made the remark, in 1911, (p. 195), that the unincorporated humus usually consists of two different strata, one upper, with plant remains retaining more or less of their structure, and one lower, mostly dark colored, with few discernable plant fragments. These horizons were designated by Hesselman in 1926 with the letters *F* and *H*, which are abbreviations of Swedish words, but which could very well be adopted for international use, at least in English, letting *F* read *fermentation horizon* or *first decomposition layer* and *H* *humified horizon* or *heavily decomposed layer*.⁹ This distinction is rapidly becoming popular, and for good reason. It is very useful in describing and characterizing different types of humus layer.

Reverting to the question of types, last year brought two contributions which seem more important than anything else which has appeared in the field for a long while. It so happens that both came from P. E. Müller's country, which thus has made up a little for its long indifference. One is a short paper by a young Danish forester, Juncker ('30), the other an elaborate monograph on the fauna of Danish forest soils by Bornebusch ('30a). Just as Hesselman in Sweden, both have grasped the fundamental idea of P. E. Müller that the classification should refer to the humus layer, to the whole natural unit, and not to arbitrarily selected constituents.¹⁰

Juncker ('30) distinguished in spruce plantations in Denmark between three types of unincorporated humus: the *poorly humified*, the *amorphous* and the *fibrous* type. It is necessary to give briefly the characteristics of these types, as the article is entirely in Danish.

In the *poorly humified* type, the decomposition is held up in its early stages. The brownish, often rather loose and unconsolidated deposit mostly shows the plant structure. Only in its lowest part, where moisture condi-

⁸ It should be noted that Sernander himself, although responsible for having used *mår* in this sense in his academic lectures, hesitated in having the term officially agreed on in this sense (Ekström, '29, p. 6).

⁹ This would seem better also in German than calling the *F*-layer *Moderschicht* (Krauss, '30) or simply *Moder* or *Auflagemoder* (Vater, '28), lest *Moder* be banished altogether as the designation of a particular humus form. The *Moderschicht* consists as a rule rather of raw-humus-like material than of *Moder* as defined by Albert ('29, Tschermak, '30).

¹⁰ It is true that Bornebusch occasionally offends a little against this principle in his nomenclature.

tions are better, rapid decomposition might occur. The underlying mineral soil, frequently sharply delimited, might be impregnated with organic matter, but is compacted. Little amorphous humus matter is formed, and the podsolizing effect is weak. This form is probably common under young, dark stands in a climate that is not too moist. It is the least dangerous form of humus accumulation, but might initiate a development to a worse kind.

The *amorphous* humus layer is black to dark brown, the decomposition being held up in its later stages. Certain substances are accumulated in the form of acid colloids. This is probably the strongest podsolizing type.

The *fibrous* humus layer is, in contrast with the other two, tenacious, felted together by roots and mycelia. The whole deposit appears imperfectly humified, and decomposition is held up from its first stages. This type seems to be particularly associated with an abundant ground cover of *Vaccinium*, etc.

The *poorly humified* type is probably immediately recognized by foresters in this country as a common plantation type. Of the other two types, which in an interesting way recall Emeis' classes 2 and 3 from 1875, the *amorphous* type is immediately recognized by anybody knowing the thick, well developed hemlock humus or spruce-balsam-humus of the mountains. An equally well developed *fibrous* type will, for natural reasons, be more difficult to visualize for many Americans, but it is immediately familiar to any person knowing anything about forest soils in northern Scandinavia.

Bornebusch's ('30a) contribution is in many respects very different from Juncker's; two of the differences stand out in the present connection. The former's new contributions largely concern the mull group, and his types are more specific and brought into closer relation with the vegetation. Bornebusch follows P. E. Müller and Hesselman in including also layers of unincorporated humus, but otherwise of mull character, in the mull group. To distinguish these from the classical mull, he names them *surface mull*. One such type is the *spruce-Oxalis-mull*, so named from the vegetation with which it is associated. This scheme is applied generally, as in the author's earlier papers.

Summing up the present situation, workers in forest soils evidently feel the need of a system of classification of the natural humus layers, or at least of types of humus. P. E. Müller's distinctions have generally been accepted as a starting point, but there is no agreement as to their further development. The actuality of the problem is evidenced by the appointment of an international committee to work on the question, following a move by Bornebusch ('30b) at the International Congress of Forest Experiment Stations in Stockholm in 1929. Such a committee was also appointed at the second International Congress of Soil Science held in Russia in 1930 (Int. Soc. Soil Science, '30).

Proposed Classification

MAIN GROUPS

For historical as well as other reasons, it seems to the present authors as if the best way out of the present confusion would be to retain Müller's division into two main groups, subdividing these groups appropriately to suit the needs of further distinction. Both these groups include many different forms, and the difference between the groups is not sharp, because transitional forms exist. The first disadvantage can be easily remedied, however, by putting in a suitable number of subtypes; the second could not be avoided any better by using three or more main groups instead of two. On the contrary, it seems to the present authors to be apparent, especially from the vegetation of the different types of humus, that the most natural dividing line runs about where P. E. Müller drew it. This seems to be true for American as well as for European conditions, if the two groups are defined in accordance with Müller's conception of them, later followed by Scandinavian authors, particularly Hesselman and Bornebusch. This implies that in the characterization of the groups the principal weight is given to the general morphology, so that unincorporated humus layers having mull characteristics are included in the mull group.

The distinctive features of the *mull* would be its crumbly or granular structure and its diffuse demarcation, the humus being either incorporated or unincorporated. The other main group would include all forest humus layers which consist of unincorporated humus, not mull-like enough to be included in the mull group. These layers are usually sharply delimited from the mineral soil, unless this has been impregnated with organic matter by the downward passage of humus, as in the typical heather profile (of Danish heaths, etc.).

There seems to be every reason for adopting *mull* to designate the first group. This term is already rather firmly established internationally, and has never been seriously misused officially. It is difficult to propose a good word for the other main group. It should preferably be short, like *mull*, otherwise the composite terms to designate subgroups or subtypes would be too awkward. P. E. Müller's *mor* fills this requirement, and historical grounds favor adopting it internationally; but unfortunately it has become a confused term due to Sernander and Hesselman, and furthermore, for linguistic reasons, does not seem very fit either in English or in German, among other reasons because of its resemblance to *moor* and *Moor*.¹¹ *Peat* is unfit as a designation for the entire group. *Raw humus* is only slightly better, has two syllables too much, and is badly confused due to the combined efforts of a number of authors (see above).

¹¹ It is true that *Moor* or *Waldmoor* has already been used in Germany as more or less synonymous with *mor*.

After considering different possibilities, the authors have decided to propose the American *duff* as an equivalent in English to P. E. Müller's *Mor*. It is a short, easy, and familiar word, and its former use as a forest term is hardly a serious objection, because the word does not seem earlier to have had a very fixed meaning. It has been listed officially (U. S. Dept. Agric., '05) as a synonym to litter, and by Hawley ('29, p. 307) as largely synonymous with Hesselman's F-layer; but in actual use the word seems mostly to stand for that blanket on top of the mineral soil which eventually can catch fire. In other words, it seems to be about synonymous with litter plus unincorporated humus. For this, there is another and more consistently used term, *forest floor*. For duff in Hawley's sense there is Hesselman's term F-layer, already introduced into American literature (Stickel, '28, Griffith *et al.*, '30). As a synonym to litter, the word is hardly needed either. Little harm would be done, it seems, in accepting the word as a group name for unincorporated humus layers belonging to the *Mor* type of P. E. Müller. In the following, duff is used in this sense.

SPECIFIC TYPES

For the further subdivision, as well as for the distinction of the main groups, the leading principle should be to obtain as far as possible a natural classification. This principle is easier to express than to follow, particularly in a region where intermediate forms play a very considerable rôle, as in the northeastern United States. But even if the types proposed should prove later to be descriptive rather than natural types, one will no doubt do well to strive from the beginning for a natural classification.

P. E. Müller, as well as his predecessor, von Post, aimed at a *genetic* classification. In doing so, they paid particular attention to the organisms active in the formation of the natural deposit. Their main concern, however, was to grasp the natural types of humus layers, whatever their genesis may be. They were quite clear about the difficulty of determining the causative agents, and very cautious in their discussions about any particular agent being responsible for the characteristics of the type. In the names given to the types, both authors more frequently refer to the general conditions of formation than to the formative agents. Müller's name "insect mull," given on rather loose grounds, was an isolated slip.

The difficulty of attributing an essential rôle to a particular organism or group of organisms still exists. Yet, the naming of types of humus after characteristic plants (or animals) is in itself sound, whether these plants (or animals) are particularly important genetically or are merely indicators of a particular type. As already mentioned, Bornebusch has recently followed this scheme. Only, there are very few species—if any—which under every condition are characteristic of a definite type of humus layer. For instance, the hemlock, like the spruce, has a marked tendency to build up a

heavy duff, but under certain conditions it may have much better humus forms. In a lime-influenced tract, it has been seen to produce an earthworm mull. A designation such as *hemlock humus* would therefore evidently never be sufficient to designate a well defined type of humus layer. The definition, and the name, must contain a further characteristic of the humus form referred to, so as not to include altogether different things, and then much depends on this further characteristic. *Hemlock duff* would by chance in general correspond to a rather definite and characteristic humus form. Only, the hemlock duff is hardly sufficiently different from much of the *spruce-balsam duff* of the mountains to warrant its being distinguished as a separate type. Thus, although *hemlock duff* would be a rather good type locally, it would not be good for general use, not even for the whole of New York State. Evidently, *conifer duff* would not do either, because this would take in too many other things besides the particular type referred to: usually heavy, but not very tenacious, with a relatively thin F and a heavy, compact, macroscopically almost amorphous H-layer, greasy to the touch.

The soundest and most logical scheme seems in principle to be both to distinguish and to name the different humus types from their own morphological and other characteristics. For instance, the type of duff just referred to could be called *greasy duff*, until something better is devised. Of course, this principle does not need to be applied dogmatically. In certain cases no doubt a designation referring to some characteristic conditions of formation or occurrence or some characteristic associated organism might serve just as well or better.

Thus it would seem rather unimportant whether the classical prototype of the mull so well characterized by Müller is called *earthworm mull* or something more non-committal. Even though the earthworms as a group are not so exclusively characteristic of this type as it seems from direct ocular study of different humus layers (Bornebusch, '30a), they are certainly characteristic enough to justify the designation earthworm mull, or why not simply *worm mull*. The authors prefer, however, to designate it by the morphological term *crumb mull*.

It is quite different with the *insect mull* of Müller. This was tentatively characterized as such on rather loose grounds (see above), and no further evidence has been obtained since Müller's time to support that idea. On the contrary, we now know that there is an abundant fauna of small arthropods also in the duff (Bornebusch, '30a). The term *insect mull* ought, therefore, to be dropped. A designation is certainly needed, however, for unincorporated humus forms of a mull character. Such forms occur in the north-eastern hardwood forests in this country, developed to rather characteristic humus layers supporting a much richer vegetation than do the ordinary forms of unincorporated humus. The authors propose the name *detritus mull* for this type, since the high content of organic matter is just as characteristic as is the structure.

The definition of the *detritus mull* would be: A deposit of unincorporated humus with some admixture of mineral soil and consisting mostly of an H-layer having a pronounced finely granular structure and a diffuse lower boundary. In the North American forms to which the term refers, the granules are small, of the order of magnitude of 1 mm. or even less. The type would seem to include also Bornebusch's *spruce surface mull* ('30a, Pl. 16) and, judging from descriptions, at least part of the *Alpenhumus* or *Alpenmoder*, perhaps also some other *Moder* types.

In the northeastern hardwood forests, this type occurs best developed in edaphically favored localities, but where conditions still do not permit a crumb mull to develop. It is natural, under such conditions, that somewhat intermediate forms should occur, *e.g.*, humus layers having the structure of crumb mull and containing many earthworms, but with an abnormally high humus content. However, forms really intermediate between crumb and detritus mull, so as to make classification difficult, seem to be remarkably rare, in spite of the fact that the former occurs also edaphically on water-influenced slopes, etc., even at higher elevations in the mountains of New York and New England.

There is one type of mull, however, already mentioned by Müller, which has the general character and relatively low humus content of the crumb mull, but considerably finer structure. Müller found this type in localities where the large earthworms were absent. The authors have found it desirable for descriptive purposes, if not for anything else, to distinguish this type from the crumb mull, but have not been able to find a better name for it than *grain mull*.

In the northeastern United States, a complex type of humus layer not infrequently occurs, where the upper part has the character of more or less matted detritus mull or the root duff to be described presently, but where the lower part is a good mull, either grain mull or even crumb mull. This situation occurs so frequently that the authors have felt the need of a word to designate it: *twin mull*.

One of the greatest difficulties of classification in the region studied is the delimitation of the detritus mull from some forms of duff. There seems to be a complete series of transitions between the friable detritus mull, without any noticeable root concentration, to forms of an unquestionable duff character. Some of the transition forms could appropriately be called *matted detritus mull*. There seems to be strong reason, however, for distinguishing, under a more expressive name, one intermediate type common in the ordinary northeastern hardwoods on not especially favored localities. The humus layer of this type has the general character of a thin duff. It is strongly matted together by a great number of roots. The root-humus mat covers the mineral soil like a carpet, with a rather distinct line of demarcation. The F-layer is very little developed, however, and the H-layer has a fine granular structure, like fine saw dust. Practically all of it can be easily

shaken out of the root mat, leaving most of even the finest ramifications of the abundant net work of roots practically clean. An appropriate name for this type of humus layer appears to be *root duff*. It seems to form a true hyphen between the mull and the duff group, but should be included in the latter because of its general character. Also the character of the vegetation it carries favors its inclusion in the duff and not in the mull group. Like the other forms of mull, the detritus mull usually carries a rich herbaceous vegetation, with a number of spring flowers as characteristic constituents. The root duff supports a much poorer herbaceous flora, lacking the characteristic spring aspect of the mull vegetation.

A more pronounced duff form closely related to the root duff is also of importance in the northeastern hardwoods. Here the upper part of the root mat includes material which is much more raw in character, leaves or fragments of leaves in different stages of decomposition. That is to say, the F-layer is better developed. It has a more or less laminated structure due to the leaves. This type much recalls some little fibrous, thinner forms of Danish beech duff. An appropriate name for the type seems to be *leaf duff*.

With the more advanced duff types, the authors would suggest a classification along Juncker's lines. For the present, his scheme has been followed altogether, dividing all the forms of heavy duff encountered in the region into two types, *fibrous duff* and *greasy duff*, the former corresponding to Juncker's fibrous and the second to his amorphous type. Juncker's poorly humified type, which also occurs in the region in dense younger pine stands, etc., has been left out for the present, because it is apparently confined to plantations and old field stands and appears not to be a stable natural type. It seems logical to start a study of humus layers with more or less stable natural conditions.

The *fibrous duff* is tough, *i.e.*, tenacious, but not necessarily dense and compact. The F-layer is well developed. The type seems to be particularly associated with the occurrence of *Hylocomia* and *Ericaceae* (*Vaccinium*) and is the dominant type, *e.g.* in northern Sweden (see Hesselman's figures 8, 9, '17b, pp. 945 and 946). In the region of United States studied, it is far less important.

The *greasy duff* is well represented by the typical heavy hemlock duff and the spruce-balsam duff of the mountains in New York and New England, often attaining a thickness of 3 dm. (1 foot) or more. The F-layer is usually relatively little developed, most of the deposit consisting of a heavy H-layer which is compact, but not very tough, and at least in its lower part muck-like, highly colloidal, greasy to feel when wet, and shrinks considerably upon drying, *e.g.* to $\frac{2}{3}$ of its original linear dimensions.

The specific types given are not supposed to cover every possible variation which can be found, in the region or elsewhere. It is rather evident, *e.g.*, that Hesselman's *mossmylla* or *mår* does not well fit into any of the above

types. This type has not been taken up because as yet the authors have not found anything in the region studied which would seem to correspond with it. If the type is met with later, it has simply to be added to the list (it could be called, for instance, *spongy duff*).

The above list should then be taken as a simple enumeration of specific types which have been considered sufficiently characteristic to be recognized as such, and there is room for any new type which might be recognized in the future. This seems to be the only workable way of developing any classification aiming at a somewhat "natural" system. Proceeding the other way drawing up a scheme in which everything to be found in the future is supposed to fit, is likely to lead to a highly artificial classification.

The following synopsis gives in condensed form the proposals made above.

SYNOPSIS

- A. Mull.* A porous, more or less friable humus layer of crumbly or granular structure, with diffuse lower boundary, not or only slightly matted.
1. *Crumb mull.* A coarse-grained mull, inhabited by large earthworms, usually in large numbers. This is the classical prototype of the mull group. Content of organic matter usually around 10 to 20 per cent or even lower, rarely over 30 per cent. Rich herbaceous vegetation, in which a spring flora of geophytes such as *Corydalis*, *Mercurialis*, *Anemone*, *Arum* (Eu.), *Dicentra*, *Dentaria*, *Hydrophyllum*, *Claytonia*, *Arisaema* (Am.), enters as a characteristic element. Litter of loose leaves, or at times practically none because of the rapid decomposition.
 2. *Grain mull.* Differs from the crumb mull by its finer granular structure and the absence of *large* earthworms. Flora like the preceding, but mostly poorer.
 3. *Twin mull.* A complex type of humus layer, consisting of one upper stratum with the characters of matted detritus mull or root duff (see below), underlain by grain or sometimes crumb mull. Flora poorer than on the preceding types, but includes mull plants.
 4. *Detritus mull.* A finely granular mull, rich in organic matter (usually over 50 per cent), looking like black saw dust. Flora variable, but always including mull plants.
- B. Duff.* A humus layer of unincorporated humus, strongly matted or compacted, or both, distinctly delimited from the mineral soil, unless the latter has been blackened by washing in of organic matter. Flora usually completely lacking typical mull plants.
5. *Root duff.* F-layer poorly developed, usually practically absent. Humus of the H-layer finely granular, like detritus mull; when dry, it can practically all be shaken out from the dense root mat which holds it together. Essentially a hardwood type.

6. *Leaf duff*. Laminated F-layer of matted leaves, H-layer much like the preceding. A hardwood and hardwood-conifer type.
7. *Greasy duff*. F-layer usually relatively little developed, often more or less fibrous, H-layer thick (usually 1 dm. or more), compact, but usually not very tough, partly or entirely black, muck-like, with a greasy feel when wet, shrinks strongly upon drying.
8. *Fibrous duff*. F-layer well developed; entire humus layer fibrous, more or less tough, but usually not very compact, showing little shrinkage upon drying. The flora of the most typical forms includes *Hylocomia* or *Ericaceae* (particularly *Vaccinium*), or both.

Distribution of Types

A visitor from abroad who is taken around to visit the forests of the northeastern United States might easily enough get the impression that typical mull is very rare in the region. In fact, it is rare in the important forest districts. On the other hand, the crumb mull, the classical prototype of the group, is very common in the small and scattered remains of the original species-rich hardwood forests on the plains, *e.g.*, in New York State on the Ontario plain and in the valleys. Indeed it seems to be the most common type in these woodlots. Its scarcity in the forests of today as a whole is very likely due simply to the fact that the best hardwood soil has largely been cultivated and transformed into agricultural land. Probably the crumb mull was originally dominant over large stretches just as one would beforehand have expected from analogy with the hardwood belt in France, etc.

Also outside the plains, the crumb mull is not infrequently met with, for instance on the New York-Pennsylvania plateau; and it can be found as isolated oases among altogether different forms of humus high up in the mountains, *e.g.*, at the 700 m. (2,100 ft.) elevation in the Green mountains. Its distribution in these regions, where it is not the dominant type, gives interesting evidence as to the factors controlling its occurrence. The controlling factor seems to be the ground water conditions, the importance of which as influencing the type of humus layer has been stressed by P. E. Müller (1887, pp. 44-45), Hesselman ('17a, chapter 10; '26, pp. 357-359), Lundblad ('27), Tamm ('29) and others. The writers have a number of cases on record which show this very clearly. The lime content of the soil is probably another important factor in the region, just as it has appeared to be in Europe, although, with the data at hand, this is not as evident as the influence of water conditions. It seems likely that the extensive lime-influence on the Ontario plain, etc., is a factor partly responsible for the frequent occurrence of crumb mull there. The most extensive areas continuously covered with crumb mull have been found on soil rich in lime (Camillus and Fayetteville, N. Y.). A third factor which has been found in Europe to be of importance is the soil texture, the mull being less common on sand

than on loam and clay (Müller, 1887, p. 44). In fact, the authors have thus far found it on pure sand only in one place (Fulton, N. Y.). The relatively high lime content could account for its occurrence in this locality, but the case is a little suspicious.

In the region studied, as well as in Europe, the crumb mull is mainly a hardwood type, but can sometimes persist also under white pine (Chestertown, N. Y.). It has even been found, in a lime-influenced tract, Fayetteville, N. Y.), under pure hemlock (compare Tamm, '21, on mull under spruce on hyperite mountains in Sweden). In the hardwoods, the authors have frequently made the observation that the stands with mull contained a smaller proportion of beech and more hard maple, etc., than those with duff. Certain more exacting species, such as basswood (*Tilia americana*) and white ash (*Fraxinus americana*), seem in New York to be strongly correlated with the occurrence of crumb mull. These correlations might of course be due simply to the fact that both these species and the crumb mull are rather "exacting" under the given conditions, but it is not impossible that the differences in the tree cover are a factor in creating or maintaining mull conditions. Data with some bearing on this silviculturally very pertinent question will be presented in a forthcoming contribution by Max J. Plice of Cornell University.

Although falling outside the scope of the present paper, it might be mentioned that, according to observations by one of the writers, the crumb mull seems to be the normal humus layer in the redwood flats in the fog belt in California; also in the Douglas fir types along the coast, mull forms were commonly observed.

The distribution of the grain mull and the twin mull has not been sufficiently studied as yet. The types have been found here and there, apparently under conditions favoring a mull but still not favorable enough to permit a crumb mull to develop, *e.g.*, on drier knolls in areas mostly covered with crumb mull, or conversely in depressions in areas with root duff dominating.

The detritus mull has been found mainly in favored localities (slopes) in the mountains, but in the northern Lake States did not seem altogether confined to such locations, although there also the favoring effect of slopes and high water-table is evident. The observations collected thus far hardly warrant any more detailed discussion.

The *root duff* seems to be the dominant form over considerable areas in the ordinary northern hardwoods, on the hills and hillsides of the New York-Pennsylvania plateau, etc., and also partly in the mountains, both in New York and New England. In the mountains, however, the duff is frequently more developed so as to fall in under *leaf duff*.

Of the more pronounced duff forms, the *fibrous duff* hardly occurs in the region in such an extreme development as for instance in north Sweden. This is quite natural, inasmuch as moss-*Vaccinium*-rich forest types are scarce

over most of the region. If anything like the north Swedish spruce-blueberry-duff is to be found in the region, it is probably in moss-rich softwood forests far north, *e.g.*, in Maine. More or less clear fibrous types do occur, however, also further south, *e.g.*, in softwood forests in the Adirondack region.

The *greasy duff* seems more important in the region. It appears to be the dominant type in several forests of pure and mixed softwoods in the mountains of New York and New England. Also the hemlock duff in lower elevations, when well enough developed, is of this type.

Data Collected on the Types

Most of the localities studied in some detail are in the northeastern states. In the field, descriptions of the profile, stand and ground vegetation were made, and samples were taken for further study, mostly of the whole profile, in some cases only of the humus layer. The vegetation analyses were either made according to Raunkjær or simply by estimating the degree of cover according to Hult-Sernander. In a number of cases, because of lack of time, the plants were simply listed without giving frequencies or degree of cover. The laboratory work included determinations of loss on ignition, pH and total lime, nitrification tests and some mechanical analyses according to Bouyoucos ('27, '30). The laboratory data for the samples of humus layer, and the distribution of some chosen plants on selected types are given in tabular form. Most of the analytical data reported on are assembled in the main Tables VII–XI at the end of the text.¹²

Some of the types, especially the root duff, are too weakly represented in the material, whereas the crumb mull is relatively over-represented. This is due to a natural tendency of the authors during the field work to concentrate first on the clearest types. The types now proposed of intermediate forms of humus have only crystallized gradually in the course of the work. For different reasons, last summer could not be used for supplementing the material of these under-represented types. Practically all the samples from the summer of 1930 were taken by Mr. C. Heimbürger, mainly in the Adirondacks, in connection with his studies on forest types. These studies concentrated during the time on the pure and mixed softwood types and practically all of the humus samples represent different shades of greasy and fibrous duff.

Some of these Adirondack forms are apparently more or less "critical," and the authors much regret not to have been able thus far to visit the localities where they were collected. It seems particularly that in higher elevations in the Adirondacks there are forms of humus more or less intermediate

¹² An appendix, not included in the present paper because of lack of space, will be made available in mimeographed form and sent to interested persons upon application to the authors. It contains descriptions of chosen localities including vegetation and soil notes, Bouyoucos analyses, etc.

between greasy duff and detritus mull, so as to make classification difficult (cf. the variations in the European *Alpenhumus* according to Leiningen, '08-'09).

METHODS USED

In the Raunkiaer analyses, a simple ring of 0.1 m.² area with radii dividing it in sectors of 5, 2, 2 and 1 dm.² area was used instead of the collapsable apparatus of Raunkiaer ('18). The latter has the disadvantage of having only one of the comparison areas (1 dm.²) definitely circumscribed, so the rest have to be guessed at. The full circle with radii takes better advantage of the principal strength of the Raunkiaer method of determining cover (see Romell, '30, p. 594). In a given locality, 25 throws with the ring were made evenly distributed as far as possible within the area chosen for analysis by spacing them one or two steps along estimated straight lines. By not looking at the ring when it was deposited, subjective choice was further eliminated. This simple method appears to be altogether sufficient for the purpose.

The Hult-Sernander degrees of cover (Du Rietz, '30, pp. 396-397) are supposed to have the following significance:

Cover index.....	1	2	3	4	5
Covering.....	0- $\frac{1}{16}$	$\frac{1}{16}$ - $\frac{1}{8}$	$\frac{1}{8}$ - $\frac{1}{4}$	$\frac{1}{4}$ - $\frac{1}{2}$	$\frac{1}{2}$ -1 of the area

The pH was determined on fresh samples, except in the few cases where there is a D meaning "dried sample" after the pH number in Tables VII to XI. Electrometric determination with the quinhydrone electrode has been used throughout. The hydrogen electrode has been tried sometimes for comparison; the values mostly checked within 0.1 pH unit. As thick a suspension was used as could conveniently be handled.

The total lime has been determined largely with standard methods, either gravimetrically or (mostly) titrimetrically. Recently, a procedure obviating the precipitation of iron and aluminum has been adopted. This method will be described by Mr. G. Cavetz in another place. Up to sample No. 218, the extraction of the lime was done by digesting the ignited soil 12 hours with constant boiling HCl on the water bath. In all the following determinations, the finely powdered ash has been dissolved in hydrofluoric acid.

The total lime is of less interest in the present connection than the absorbed lime, and a number of determinations of the lime extracted with ammonium chloride solution from the unignited sample has been made. With some of our material, however, even with samples very poor in lime, it proved difficult to get a reasonably distinct end-point, and these determinations were stopped pending a study of methods. No figures on adsorbed lime are therefore reported in the present paper.

The loss on ignition was determined by heating to 550° C. in an electric furnace, after the sample had been dried to constant weight at about 100° C. (in a steam oven or for the last few samples in an electric vacuum oven).

The loss on ignition is taken as a measure of the humus content, although of course it includes the chemically combined water. This is believed to be sufficiently accurate for the present purpose.

The nitrifying power of each humus layer was determined by storage tests according to Hesselman's technique, without any addition. The tests ran 3 (in one series 4, cf. notes to Table V and VII-XI) months at room temperature, about 20° C. In general, an amount of the sample corresponding to 25 grams dry weight of *humus* (not of soil) has been used, except for the typical mulls, where as a rule half the amount was used. The samples were stored in 1 liter Erlenmeyer flasks, cotton plugged, with enough water added to bring the moisture up to what was considered from pure inspection as about the optimum content. Water was also added at intervals during the test to make up for the losses by evaporation (determined by weighing). We refrained from trying to standardize the water content more accurately, partly because a satisfactory common standard is difficult to find for widely different humus forms, partly because there seems to be a fairly wide optimum range for the moisture content, as shown in the following, in which the values in the last two columns refer to mg. of nitrate-N formed in 3 months per kg. of humus:

Moisture in % of water capacity	Sample 304 I Crumb mull, Jacksonville	Sample 304 II Root duff, Jacksonville
40	132	1095
50	3530	1135
60	3580	1285
70	3520	1485

When preparing the samples, roots and pebbles were cleaned out, but otherwise the samples were tampered with as little as possible. They were either not sieved at all, or only through a coarse (5 mm.) flamed sieve on a clean paper.

The nitrate content was determined by the phenoldisulphonic acid method, using Chamot's ('11) formula for the reagent. The samples were extracted with water for about half an hour (cf. Blom and Treschow, '29, pp. 183-184), and the filtrate cleared with caustic lime. In a few cases neither lime nor Harper's ('24) clearing mixture yielded color-free solutions. It was found possible in such cases to destroy the humus color with hydrogen peroxide without apparent loss of nitrates. The nitrate content at the start of the test was determined in a parallel sample, and the figures given for nitrification are the differences between the end and beginning values. The latter have not been deemed to have any interest in themselves, because the determinations could rarely be made on absolutely fresh samples (usually, several days, a week or even more, elapsed between sampling and analysis), and are not reported.

Parallel with the storage tests, inoculation tests were made with a number of samples, using a modified Winogradsky's nutrient solution about 1/50-n

with respect to ammonia, and with calcium carbonate as a buffer instead of magnesium carbonate (50 ml. portions in 500 ml. Erlenmeyer flasks). About 1 cc. of material (measured with a small porcelain spoon) was used for inoculation. The course of the nitrification was followed by drop tests with diphenylamine reagent according to Harvey ('20), Nessler's and sometimes also Trommsdorff's reagent (very seldom needed, because nitrites are rarely accumulated when CaCO_3 is used as the buffer). In the first series, the strength of the reaction was only estimated; later the test was made roughly quantitative (cf. Romell, '28, p. 58; Morgan, '30).

VEGETATION

Since lack of space prevents the inclusion of the vegetation lists secured, only a very summarized account of the occurrence of certain plants on crumb mull, detritus mull and root duff is given in Table I. The choice has

TABLE I. *Distribution of some plants on crumb mull, detritus mull and root duff*

The figures give frequencies of occurrence computed on the basis of 10 localities in every group. The actual number of localities included in the statistics is 19 for the first, 5 for the second and 6 for the third group.

Plants		Crumb mull	Detritus mull	Root duff	Mull plants, continued	Crumb mull	Detritus mull	Root duff
Duff plants	Lycopodium lucidulum.....	0	4	3	Dicentra canadensis.....	4	2	0
	Lycopodium obscurum.....	0	0	2	Dicentra cucullaria.....	2	0	0
	Majanthemum canadense.....	1	4	8	Hepatica acutiloba.....	3	0	2
	Mitchella repens.....	1	0	7	Hydrophyllum canadense.....	2	0	0
	Trientalis americana.....	1	2	3	Hydrophyllum virginianum.....	2	0	0
Trees	Trillium undulatum.....	0	0	2	Impatiens biflora.....	4	4	0
					Osmorhiza Claytoni.....	5	2	2
	Fraxinus americana.....	6	4	5	Osmunda Claytoniana.....	2	2	0
	Liriodendron tulipifera.....	1	2	0	Podophyllum peltatum.....	4	0	0
	Tilia americana.....	4	2	2	Prenanthes altissima.....	3	2	0
Mull plants					Ranunculus abortivus.....	3	2	0
	Actaea alba.....	7	2	2	Sanguinaria canadensis.....	2	2	0
	Arisaema triphyllum.....	5	4	2	Trillium erectum.....	4	4	0
	Asarum canadense.....	2	4	0	Trillium grandiflorum.....	4	0	2
	Carex plantaginea.....	3	0	0	Viola canadensis.....	4	0	0
	Caulophyllum thalictroides.....	4	2	0	Viola pubescens.....	3	0	0
	Circaea lutetiana.....	3	0	0	Viola scabriuscula.....	2	2	0
	Claytonia caroliniana.....	3	0	0	Viola sororia.....	2	0	0
	Dentaria diphylla.....	4	0	0				
	Dentaria laciniata.....	2	0	0				

been determined by two considerations. First, it is of particular interest to get a certain check on the value of the new intermediate types and eventually find species sufficiently correlated with them to serve as indicator plants. Second, the classification is somewhat uncertain for a good deal of the material of the fibrous and greasy types of duff. Since only such localities

could be used, for which reasonably good and complete vegetation notes are available, the twin mull and leaf duff became too poorly represented, and are therefore excluded.

Although unfortunately the material is small for the detritus mull and root duff, some interesting facts stand out rather clearly from the table. As would be expected, the detritus mull is truly intermediate between the crumb mull and the root duff, but there is a slight majority for the cases in which it is closer to the crumb mull than to the root duff in the statistics. In reality, several of the spring geophytes which, from the table, appear to be characteristic only of the crumb mull do actually occur also on detritus mull, but hardly on root duff. Their absence on detritus mull in the table is due to insufficient material.¹³

It is difficult at present to list any species sufficiently characteristic for the more specific types, but it is easy to see that a number of plants within the region are more or less strictly confined to mull. Most of them are spring geophytes, a biological group which also in Europe is characteristic of the mull. Some are nitrate plants (*Circaea*, *Impatiens*, *Prenanthes*, violets). Most of the good mull indicators are listed in floristic books as occurring "in rich woods," "rich, damp woodlands," etc. No doubt it would be both a better and a shorter characteristic to say "mull plants." It can frequently be noted, that these plants in general seem to prefer moist sites, but where mull occurs on drier sites, they can be found there as well.

Other plants are characteristic of duff and occur on mull rarely or not at all, e.g. *Coptis*, *Cornus canadensis*, *Trillium undulatum*, *Lycopodium lucidulum* and *obscurum*, *Mitchella*, *Majanthemum*, and *Trientalis*. The most pronounced duff plants do not figure in Table I, because they are scarce or absent even on the root duff. *Trientalis* seems to be a better duff indicator in Europe than it is in northeastern United States.

Besides these plants which are more or less characteristic of certain types of humus layer, there are of course others which have a wide range and occur in widely different types. Such species are, e.g., *Oxalis*, *Aralia nudicaulis*, and *Smilacina racemosa*.

HUMUS CONTENT

A table of correlation between type of humus layer and per cent loss on ignition ("humus" content) shows a very wide variation within most types (Table II). Morphologically and floristically distinct types might show little or no difference with regard to humus content (cf. detritus mull, root duff and leaf duff in Table II). The most pronounced duff forms, of course, almost invariably show a very high humus content, at least of the F-layer. The crumb mull, on the other hand, as a rule has a humus content below 20

¹³ On the other hand, one or other species (e.g., *Viola pubescens*) appears from the table to be an exclusively mull plant, although it actually has a wider range and can also be found on root duff.

per cent. Still, according to the authors' findings, the American forms of crumb mull are as a rule richer in humus than typical European forms. For the latter, P. E. Müller (1887, p. 66) gave the figure 10 per cent as a maximum value. Most of our samples lie between 10 and 20 per cent.

TABLE II. *Distribution of samples according to "humus" content (loss on ignition)*

Humus type	"Humus" content, per cent									
	0-10	11-20	21-30	31-40	41-50	51-60	61-70	71-80	81-90	91-100
Crumb Mull.	11	22	9	1	2					
Twin Mull, upper.			2	1	1					
Twin Mull, lower.		3	1							
Detritus Mull, upper.						2	1	2	2	
Detritus Mull, lower.				3	4	1			1	
Root Duff, upper (F).					1		1	1	5	1
Root Duff, lower (H).			1		1	2	6	2		
Leaf Duff, upper (F).								1	3	4
Leaf Duff, lower (H).				1		2	2	1	2	1
Greasy Duff, upper (F).							1	2	5	17
Greasy Duff, lower (H).				2	1	3		6	12	19
Fibrous Duff, upper (F).					1				2	11
Fibrous Duff, lower (H).					1	1	2	2	3	5

This is the only real difference which the authors have been able to find between American and European crumb mull. In all other respects, the American type seems to correspond exactly with the European one. In this connection, attention might be drawn to one of P. E. Müller's statements, which could easily be somewhat misinterpreted. In his description of the crumb mull (*l.c.*, p. 9), he states as a sign of its porosity and loose structure that the feet sink in when walking over it. It is very rare, however, even in the best Danish beech mull, that the deposit in itself is as loose as that. As a rule, the feet do not sink down in the solid mull, but only when they strike one of the superficial mole-tracks.¹⁴ It is true that these tracks run close enough in a Danish beech forest with good mull, and are often remarkably parallel and regularly spaced (Bornebusch, '30a).

HYDROGEN ION CONCENTRATION

The distribution of the samples of different types of humus into pH classes is shown in Table III. Here again, there is a very considerable variation within every type, but generally speaking, there is a steady decrease

¹⁴ This point was brought out expressly by Bornebusch last summer in discussions with one of the authors.

in pH from the crumb mull to the extreme duff through the whole series of intermediate forms. Looking for details, one finds that there is less than .5 difference in the average pH between the different types classified as mull,

TABLE III. *Distribution of samples in classes of pH*

The figures at the head of the columns represent pH; the figures in the columns are the number of samples in the pH classes. Three samples of crumb mull had a pH of over 7.5 (up to 7.8).

	7.5-7.1	7.0-6.6	6.5-6.1	6.0-5.6	5.5-5.1	5.0-4.6	4.5-4.1	4.0-3.6	3.5-3.1	3.0-2.6
Crumb Mull.....	1	3	7	12	8	7	4			
Twin Mull, upper.....		1		1		1	1			
Twin Mull, lower.....		1	1	1		1				
Detritus Mull, upper....			1	2	2	2				
Detritus Mull, lower....			1	3	2	1	1	1		
Root Duff, upper (F)....			1		3	4	1			
Root Duff, lower (H)....				1	1		5	5		
Leaf Duff, upper (F)....					2	3	1	2		
Leaf Duff, lower (H)....						1	2	4	2	
Greasy Duff, upper (F)..					3	4	6	9	4	
Greasy Duff, lower (H)..							2	4	20	17
Fibrous Duff, upper (F)..						1	3	9	1	
Fibrous Duff, lower (H).							1	2	8	3

and more than .5 pH between the root duff and the nearest mull. The pH values, just as the vegetation, seem to justify the line drawn on morphological grounds between detritus mull and root duff.

NITRIFICATION

In all earlier work, perhaps the most consistent difference between mull and duff which can be ascertained by laboratory tests has been found in the nitrifying power. Reference has been made in the introduction to an old statement of Emeis to that effect, which has been essentially corroborated in recent years by the work of Weis, Hesselman and others. Even the best *Hylocomium*-humus studied by Hesselman (his "mår," cf. above), a form intermediate between fibrous duff and mull, has failed to show any nitrification in the usual storage test. Only when it has been exposed for some time on a clear cutting or in an opening in the stand, does it nitrify. At the same time it changes morphologically so as to approach a mull.

Table IV shows that this is quite different with the American forest humus layers included in the present study. Recording the nitrification with the same technique used by Hesselman and others, a considerable percentage of nitrifying samples has been found within every type of humus layer, even

the most extreme duffs. In all types, except the fibrous duff, there have even been samples with a very high nitrification (1,000 to several thousands of mg. nitrate-N per kg. of "humus" in 3 months).

TABLE IV. *Distribution of samples in classes of intensity of nitrification as indicated by the storage tests*

Nitrification in grams nitrate-N per kilogram of "humus."

	0.0	0.1-0.5	0.6-1.0	1.1-1.5	1.6-2.0	2.1-2.5	2.6-3.0	3.1-3.5	3.6-4.0
Crumb Mull.....	2	12	17	8	2	3			1
Twin Mull, upper.....			1	1	1	1			
Twin Mull, lower.....		1	1	2					
Detritus Mull, upper.....	1			1	2		3		
Detritus Mull, lower.....	1	4	1		2	1			
Root Duff, upper (F).....	1	2	2	1	1		1		
Root Duff, lower (H).....	4	4	1	1				2	
Leaf Duff, upper (F).....		4	2		1	1			
Leaf Duff, lower (H).....	4	3	2						
Greasy Duff, upper (F).....	9	6	4	4	3				
Greasy Duff, lower (H).....	26	16	1						
Fibrous Duff, upper (F).....	6	8							
Fibrous Duff, lower (H).....	7	7							

One sample of Root Duff, Upper (F) layer, showed 6.4 g. nitrate-N per kilogram of humus.

Looking closer at Table IV, a still more startling fact appears, namely, the relatively low average values for the crumb mull, in spite of the fact that the results have been expressed on the basis of *humus*, not of *soil*, so as not to disfavor types which run low in organic matter. The values not only for the less pronounced mulls, but even for the root duff, average higher than those for the crumb mull, and the values over 1,000 mg. are relatively more common in some of the types outside than they are within the crumb mull type. The absolute maximum, with the impressive value of over 6,000 mg. per kg. of humus, was found in a sample of root duff. In fact the figures as a whole seem to indicate that the root duff has about as marked a tendency to nitrify strongly as any other type.

It is evident, then, that in stored samples of forest humus layers a strong nitrification is much more common in this region than it has been found to be in Europe, and not at all confined to humus layers of a mull character.

The inoculation tests, although confirming this result in a general way, give a notably different picture in detail. A comparison of results obtained with both methods on the same samples is shown in Table V. It appears

that in the inoculation tests, nitrification is complete in all tests with crumb mull, twin mull and detritus mull. In all other groups, samples with relatively rapid and complete nitrification alternate with slowly or incompletely nitrifying samples. This is in better agreement with what the vegetation would seem to indicate, and also in better agreement with previous experience, although the latter is largely based on storage and not on inoculation tests.

TABLE V. *Comparison between results of storage and inoculation tests for nitrification*

Type of humus		Sample no.	Storage test, mg. N/kg. humus nitrified in 3 mo.*	Inoculation test						
				Weeks for nitrification					Nitrification in 3 mo.*	
				1/8	1/4	1/2	3/4	full		
Crumb mull	105	760 IV						full V		
	106	560 IV						full V		
	107	1510 IV						full V		
	108	644 IV						full V		
	123	1070						full IV		
	101	2200 IV						full V		
	122	1710						full IV		
	331	120	2		4		6	full		
	345	677	3		5	8	10	full		
	355	12	2		5		10	full		
	124	1370						full IV		
	126	730						full IV		
	130	1200						full IV		
	131	1280						full IV		
	132	1120						full IV		
	133	2240						full IV		
Twin mull		104 141	1390 IV 1300					full V full IV		
Detritus mull	Upper	315a 154 163 167	24 1190 2720 1900	2	4	6	9	10	full full IV full IV full IV	
	Lower	315b 155 158 164 168 169	303 430 1880 1980 850 250		9			10	1/2 full IV full IV full IV full IV full IV	
	F-layer	332F 346F 356F	720 1800 1000	11 6		8			1/8 1/2 full	
		H-layer	103 332H 346H 356H 134	171 IV 20 77 210 3330		8	5		12	full V 0 full 1/2 full IV

TABLE V. Continued

Type of humus		Sample no.	Storage test, mg. N/kg. humus nitrified in 3 mo.*	Inoculation test					
				Weeks for nitrification					Nitrification in 3 mo.*
				1/8	1/4	1/2	3/4	full	
Leaf duff	F-layer	334F 335F 336F 337F 340F	440 73 2520 1988 278	5 3	 3	10 5 5	 8 8	 10 10	1/2 o full full o
	H-layer	102 334H 335H 336H 337H 340H	550 IV 22 88 668 40 o	 5 5	 8 8	 10 10	 12 12	full V o o full 1/2 o	
	F-layer	119 328F 327F 317a 325F 330F 350F 362F 363F 341F 342F 343F 344F 359F 322F 351F 352F 333F	o IV 1600 30 o 1600 60 280 1720 1060 89 1000 1294 1300 760 150 750 50 70	4 4 4 4 5 5 3	 11 9 4 4 8 8 10 12 5	9 16 11 6 6 8 8 12 5	 14 14 12 (18) 10 12 10 12 14 16	o V 1/2 o o 1/4 1/2 o full 3/4 1/2 full full full o 3/4 1/2 o	
	H-layer	120 121 327H1 327H2 328H 317b-d 325H1 325H2 330H1 330H2 350H1 350H2 362H 363H1 363H2 341H 342H1 342H2 343H1 343H2 344H 359H1 359H2 322H 351H1 351H2 352H 333H	o IV o IV 60 140 20 o; o; o 20 25 20 80 68 162 31 130 40 51 o o 42 52 300 90 54 60 60 45 60 40	 o 6 8 10 5 8 12	 8 10 6	 8 12 12 6	 12 12	o V o V o o o o; o; o o o o o o full 1/2 o 1/4 o o 1/8 o full 1/2 1/8 o o o o o	

TABLE V. *Continued*

Type of humus		Sample no.	Storage test, mg. N/kg. humus nitrified in 3 mo.*	Inoculation test					
				Weeks for nitrification					Nitrification in 3 mo.*
				1/8	1/4	1/2	3/4	full	
Fibrous duff	F-layer	316a	0						0
		349F	300						0
		326F	50						0
		360F	50						0
		357F	-20						0
		364F	160			6			1/2
		365F	-35		12				1/2
		347F	213		6	8		10	full
		348F	160						0
		338F	440				10	12	full
		329F	240	5 9	11	14		16	1/4
		159	0						0 IV
	H-layer	316b	195						0
		349H	200						0
		326H	50						0
		360H	-26						0
		357H	-27						0
		364H ₁	-9						0
		364H ₂	-10						0
		365H	10						0
		347H	100						0
		348H	90						0
		338H	200						0
		329H	150		6	11		16	1/2
		160	0						0 IV

* One early series of storage tests and two of inoculation tests ran by mistake 4 or 5 months instead of 3. These values are marked IV or V in the table.

The fact that the inoculation tests have given more reasonably looking results than the storage tests is contradictory to what Hesselman ('17a, pp. 380-381) found in parallel experiments with both methods. The discrepancy is very likely due to the fact that Hesselman used the classical culture medium with magnesium carbonate as a buffer. This medium, probably because of its decidedly alkaline reaction, is not suitable for the nitrifying organisms of forest soils (Gaarder and Hagem, '28, Romell, '28), a possibility already suggested by Hesselman ('17a, p. 38).

One fact seems to be well established by the tests reported on, namely, the much wider distribution of active nitrifying organisms in forest humus layers of the region than could be expected by previous experience. Samples for which both tests uniformly indicate a marked nitrifying power occur in all types of humus. On the other hand, there are within the two most pronounced types of duff several samples for which both tests have failed to show any nitrifying power.

With regard to the relative intensity of nitrification in the different forms

of mull and the lighter duffs, there is the already mentioned discrepancy between the two tests applied and between the storage test and other indications. The probable reason for the anomalies in the storage tests is a "sampling effect" affecting some types of humus more than others. This point will be discussed in a forthcoming paper by one of the authors.

TABLE VI. *Correlation between pH and nitrification during storage*

The first column gives grams of nitrate N per kilogram of humus. The other columns are pH, and the figures in each represent numbers of samples.

	7.5-7.1	7.0-6.6	6.5-6.1	6.0-5.6	5.5-5.1	5.0-4.6	4.5-4.1	4.0-3.6	3.5-3.1	3.0-2.6
6.1-6.5			1							
5.6-6.0										
5.1-5.5										
4.6-5.0										
4.1-4.5										
3.6-4.0			1							
3.1-3.5				1	1					
2.6-3.0				2		2				
2.1-2.5			1	1	2	2				
1.6-2.0		1	1	1	6	2	1			
1.1-1.5		2	3	4	1	4	4			
0.6-1.0		2	2	7	6	2	6	5	1	
0.1-0.5	1		2	2	3	11	12	17	10	7
0.0				2	2	2	4	14	24	13

There are also 3 samples in the pH class 8.0-7.6, not shown in the table, 2 of which nitrified between 0.1-0.5, and 1 between 0.6-1.0 g. N per kg. of humus.

NITRIFICATION AND ACIDITY

In Table VI, a comparison is made between the pH of the samples and their nitrifying power, as indicated by the storage test. The picture is as interesting and as puzzling as Table IV. Evidently the active organisms have an extraordinarily wide pH range. The inhibiting acidity seems to lie at as low a pH as hardly or just barely occurs in any forest humus type in the region, and it seems questionable whether the acidity as such can anywhere be the inhibiting factor. Even in the lowest pH class, pH 3.0 and below, there are distinctly nitrifying samples. The presence of active nitrifying organisms within this pH range is indicated in two cases also by the inoculation test (cf. Table V). Nitrification in soil samples of so low pH does not seem to be earlier on record (cf. the review of literature in Gaarder and Hagem, '28, chapter 3).

Nevertheless, there seems to be a distinct correlation between pH and nitrification. Table VI indicates an optimum between pH 5 and 6, a surprisingly low range. However, if the values for the different types of humus layer are plotted separately (these tables have been omitted in order to save space) it will be seen that there is hardly any distinct correspondence

between pH and nitrification for the mulls, whereas for the duffs there is a clear correlation, which is *positive all over the range represented*. The only remaining indication of the optimum mentioned would be the surprisingly low values of the 4 alkaline samples of crumb mull. Furthermore, the inoculation tests fail to show any indication of an optimum between pH 5 and 6. All the samples above pH 5 have nitrified in culture, those above pH 5.5 nitrifying completely. In the classes from pH 5 down, there is an ever increasing percentage of non-nitrifying samples. The figures are, in order, 30, 39, 50, 86 and 88 per cent. The correlation between pH of sample and nitrification in culture is consequently positive all the way within the range represented. Here again, the inoculation tests have yielded the more reasonable looking result (cf. above). In the authors' opinion, the apparent optimum at pH 5-6 indicated by Table VI is a statistical effect due to the mixing together of various types of humus layer with different pH range and different behavior in the storage tests. If this explanation is correct, the chief interest of the table would be as an example of the mistakes which can easily arise from a mechanical statistical treatment without due regard to natural group differences within the material.

LIME CONTENT

The figures for the lime content of the samples are reported in the main Tables VII to XI below. They are given in three ways, in per cent of dry soil, of ash and of "humus" (*i.e.*, loss on ignition). In whatever way they are expressed, it is difficult to compare them in a significant way for samples of widely different humus content. They are given for what they are worth in judging the rôle of the total lime content in influencing the type of humus layer. Figures of exchangeable lime would no doubt have been more valuable from several points of view, but for reasons given above no such figures can be reported at the present time.

The very great differences found in some instances between samples from the same locality are probably due to the occurrence of local lime centers of some sort. To some extent, these variations seem to be reflected in the pH (cf. Jacksonville, Table VII).

The marked difference in lime content between the F- and the H-layer in many of the duff samples is interesting. This probably illustrates at the same time the "lime-pumping" effect of the trees and the rapid leaching out of lime under the given conditions. To a certain extent, of course, the decrease in lime content of the ash can be purely statistical, due simply to admixture of mineral soil, low in lime, in the lower horizon.

The Bouyoucos tests were carried out in the Department of Silviculture of the New York State College of Forestry by Mr. C. E. Reynolds, the other laboratory tests in the Forest Soils Laboratory at Cornell University, largely by Mr. M. J. Plice, Mrs. A. Romanoff and Mr. G. Cavetz to whom the authors wish to express their thanks. We are much indebted to Dr. C. E.

TABLE VII. *Crumb Mull*

Sample no.	Date of sampling	Location	Stand	Depth in cm.	Loss on ignition %	† pH	Nitrification in 3 months* mg. N/kg. "humus"	Total CaO		
								Per cent of dry soil	Per cent of ash	Per cent of "humus"
105	May '29	Bethlehem, N. H.	Y.B., Be., S.M.	(0-7)	14	5.6	760 IV	.26	.3	1.88
106	" "	" "	" " "	(0-7)	15	5.4	560 IV	.085	.1	.56
190a	Sept. '29	" "	" " "	0-7	13	4.9	350	.22	.25	1.68
107	May '29	Crawford, N. H.	Y.B., Ba., R.S.	0-5	21	4.2	1510 IV	.079	.1	.37
108	" "	" "	" " "	5-8	24	4.5	644 IV	.076	.1	.32
1891a	Sept. '29	" "	" " "	0-5	24	4.3	630	.44	.58	1.86
1891b	" "	" "	" " "	5-10	21	4.2	440	.12	.15	.56
1881	Sept. '29	Meredith, N. H.	R.M., W.B., Y.B., Elm	2-10	21	5.3	254	.77	.97	3.75
192a	" "	Sugar Hill, "	S.M., Y.B., Bass.	0-5	12	5.3	645	.93	1.06	7.68
101	May '29	Battell Park, Vt.	S.M., Be., Y.B.	(0-10)	49	6.3	2200 IV	.25	.5	.52
193a	Sept. '29	" "	" " "	0-10	49	6.7	730	1.0	1.97	2.03
208a	Oct. '29	Arnot Forest, N. Y.	Mixed Hardw.	2-8	17	5.6	480	1.09	1.32	6.38
122	June "	Camillus, N. Y.	S.M., Be., Elm., Hb.	0-8	12	6.3	1710	.088	.1	.72
204a	Oct. "	" "	" " "	0-10	30	7.2	470	12.9	18.5	42.3
204b	" "	" "	" " "	15-25	21	7.8	380	7.44	9.40	35.8
123	June '29	Holcomb, N. Y.	R.O., Hi.	0-6	9	6.3	1070	.091	.1	1.01
182	Sept. "	Chestertown, N. Y.	W.P., Hi., Y.B.	0-10	19	4.9	280	.89	1.1	4.72
183	" "	" "	" " "	(10-15)	8	5.1	240	1.28	1.4	15.5
209b	Oct. '29	Enfield, N. Y.	S.M., Be., Bass.	0-7	30	7.7	580	2.34	3.34	7.80
199	Sept. "	Fayetteville, N. Y.	Hemlock	(0-15)	19	4.8	920	.78	.96	4.14
201a	" "	" "	S.M., Be., Bass.	(10-15)	11	5.7	760	.65	.73	5.85

* IV = Nitrification in 4 months. † D = pH determined on dried sample.

TABLE VII.—Continued

Sample no.	Date of sampling	Location	Stand	Depth in cm.	Loss on ignition %	† pH	Nitrification in 3 months* mg. N/kg. "humus"	Total CaO		
								Per cent of dry soil	Per cent of ash	Per cent of "humus"
197a	Sept. '29	Fulton, N. Y.	S.M., Be., W.A., Hi.	0-10	9	4.9	2100	.37	.41	3.98
302a	May '30	"	" " " "	0-5	9	5.4 D	247	1.18	1.3	12.67
302b	"	"	" " " "	5-15	9	5.0 D	920	.93	1.0	13.71
303a	"	"	Bl.Ch., S.M., Be., W.A.	0-5	9	5.8 D	934	.73	.8	8.61
303b	"	"	" " " "	10-15	6	5.6 D	810	3.57	3.8	57.45
210a	Oct. '29	Jacksonville, N. Y.	S.M., Be., Bass.	0-10	17	7.7	470	1.36	1.63	8.24
3041	May '30	"	" " " "	(0-10)	16	6.4 D	3580	1.94	2.3	12.25
331	June "	"	" " " "	0-15	17	6.5	120	1.73	2.1	10.54
345	Aug. "	"	" " " "	0-15	16	6.1	677	.085	.1	.55
355	Sept. "	"	" " " "	0-15	14	6.0	12	.086	.1	.64
366	Oct. "	"	" " " "	0-15	15	5.6	1420	.085	.1	.57
368	Nov. "	"	" " " "	0-15	16	6.6	682	.084	.1	.51
202a	Sept. '29	"	" " " "	(0-10)	11	5.0	1060	.49	.55	4.66
300a	May '30	Lafayette, "	" " " "	0-10	10	6.0 D	943	1.44	1.6	14.73
300b	"	"	" " " "	15-20	7	6.0 D	649	.84	.9	12.74
306a	"	"	" " " "	1-8	34	5.1 D	-20	.4	.6	1.18
306b	"	Newcomb, "	Y.B., Be., W.A.	20-25	29	5.0	535	1.21	1.7	4.23
180a	Sept. '29	Saratoga Springs, N. Y.	R.O., Bass., S.M., W.A.	0-1	10	5.4	1690	.09	.1	.86
124	June '29	Ann Arbor, Mich.	W.O., R.O., Hi.	0-8	8	7.0	1370	.092	.1	1.21
126	"	Ruse, Mich.	S.M.	0-8	12	5.7	730	.088	.1	.71
130	"	"	"	0-5	20	5.9	1200	.08	.1	.40
131	"	"	"	(0-5)	13	5.9	1280	.087	.1	.65
132	"	"	"	(0-5)	15	6.1	1120	.085	.1	.57
133	"	"	"	0-4	13	5.3	2240	.087	.1	.50

TABLE VIII. *Twin Moll, Detritus Moll*

Sam- ple no.	Date of sampling	Location	Stand	Depth in cm.	Loss on ig- nition %	† pH	Nitrification in 3 months* mg. N/kg. "humus"	Total CaO		
								Per cent of dry soil	Per cent of ash	Per cent of "humus"
Twin mull	May '29	Battell Park, Vt.	S.M., Be., Y.B.	(0-5)	44	4.9	1390 IV	.056	.1	.13
	Sept. "	Fayetteville, N.Y.	S.M., Be., Bass.	2-4	29	4.1	900	.75	1.05	2.60
	" "	" "	" " "	0-1	29	6.6	1720	1.97	2.8	6.7
	Oct. "	Jacksonville, "	Be., S.M., W.P.	1-5	20	6.7	1460	1.64	2.06	8.0
	" "	" "	" " "	0-2	34	5.6	2170	1.42	2.16	4.15
	" "	" "	" " "	2-5	11	4.7	240	.4	.45	3.81
	July "	Cass Lake, Minn.	S.M., Y.B.	2-15	14	6.1	550	1.04	1.21	7.60
				2-10	29	5.7	1300	.071	.1	.24
Detritus mull	Sept. "	Long Trail Lodge, Vt.	S.M., R.M., Y.B., Be.	0-2	53	4.6	1980	1.69	3.60	3.19
	" "	" "	" " "	3-7	32	3.8	450	.73	1.07	2.3
	Oct. "	Baldwinsville, N.Y.	Hl., W.P., Hl., R.M.	(0-1)	80	4.6	2830	1.35	6.75	1.69
	" "	" "	" " "	(1-2)	37	4.8	2510	.89	1.42	2.38
	May '30	Hoffmann Notch, N.Y.	Y.B., S.M., Be., R.S.	0-2	89	5.4	24	1.65	14.50	1.86
	" "	" "	" " "	2-8	58	4.2	303	.84	2.0	1.44
	" "	Pack Forest, N.Y.	S.M., Bass., Y.B.	0-2	51	6.0 D	2590	1.08	2.2	2.13
	" "	" "	" " "	2-4	40	6.0 D	-21	.12	.2	.50
	July '29	Superior Nat. For., Minn.	Mixed h'dw'd	0-3	79	6.4	1190	3.15	15.2	3.97
	" "	" "	" " "	3-5	44	6.5	430	.79	1.4	1.82
	" "	" "	Y.B., S.M., W.S.	3-5	46	5.4	1880	.054	.1	.12
	" "	" "	Alder	0-3	66	5.9	2720	1.39	4.1	2.1
	" "	" "	" " "	3-7	44	5.6	1980	1.57	2.8	3.5
	" "	" "	Mixed h'dw'd.	0-3	90	5.1	1900	1.83	18.3	2.33
	" "	" "	" " "	3-10	87	5.4	850	3.02	22.4	3.5
	" "	" "	" " "	10-20	42	5.7	250	.87	1.5	2.0

* IV = Nitrification in 4 months. † D = pH determined on dried sample.

TABLE IX. *Root Duff, Leaf Duff*

Sample no.	Date of sampling	Location	Stand	Layer, depth in cm.	Loss on ignition %	† pH	Nitrification in 3 months* "g. N/kg. humus"	Total CaO		
								Per cent of dry soil	Per cent of ash	Per cent of "humus"
1891Va	Sept. '29	Meredith, N.H.	R.M., W.B., Y.B., Elm	H 0-2	56	3.9	0	.57	1.30	1.02
103	May "	Bartell Park, Vt.	Be., S.M., Y.B., Y.B.	H (-)	61	3.7	171 IV	.039	.1	.063
395a	" '30	" "	Hl., S.M., Be., Y.B.	F 0-½	88	4.2	480	.50	4.3	.57
395b	" "	Arnot Forest, N.Y.	" " " "	H ½-5	73	3.7	780	.32	1.20	.44
205a	Oct. '29	Baldwinsville, N.Y.	Be., R.M., Hl., Bl. Ch.	F 0-1	72	6.2	6440	1.73	6.24	2.4
205b	" "	" "	" " " "	H 1-2	45	5.1	3440	1.46	2.66	3.24
304II	May '30	Jacksonville, N.Y.	Be., S.M., W.P.	F (0-1)	44	5.5 D	1485	1.29	2.30	2.96
332F	July "	" "	" " " "	F 0-1	86	5.1	720	1.94	13.4	2.27
332H	" "	" "	" " " "	H -5	64	4.3	20	.90	2.5	1.41
346F	Aug. "	" "	" " " "	F (0-1)	87	4.8	1800	1.43	11.0	1.64
346H	" "	" "	" " " "	H (1-5)	65	4.0	77	.035	.1	.054
356F	Sept. "	" "	" " " "	F (0-1)	86	5.2	1000	.64	4.6	.74
356H	" "	" "	" " " "	H 1-5	73	4.4	210	.027	.1	.037
367F	Oct. "	" "	" " " "	F (0-)	86	4.6	170	1.04	7.4	1.21
367H	" "	" "	" " " "	H (-)	55	4.0	36	.045	.1	.081
369F	Nov. "	" "	" " " "	F (0-)	92	4.8	-50	.88	10.3	.96
369H	" "	" "	" " " "	H (1-5)	70	4.1	30	.030	.1	.043
184a	Sept. '29	Pack Forest, N.Y.	S.M., Hl.	F 0-2	69	4.6	2610	2.17	7.2	3.15
184b	" "	" "	" " " "	H 2-5	28	4.1	170	1.38	1.3	5.00
212a	Oct. "	Townsend, N.Y.	S.M., Be., Hl.	H ½-3	64	4.2	1170	1.21	3.36	1.89
134	June "	Ruse, Mich.	S.M., Y.B.	H (-3)	70	5.9	3330	1.23	4.1	1.76

* IV = Nitrification in 4 months. † D = pH determined on dried sample.

TABLE IX.—Continued

Sample no.	Date of sampling	Location	Stand	Layer, depth in cm.	Loss on ignition, %	† pH	Nitrification in 3 months* mg. N/kg. "humus"	Total CaO		
								Percent of dry soil	Per cent of ash	Per cent of "humus"
102	May '29	Battell Park, Vt.	Beech	F+H	65	4.1	550 IV	.035	.1	.054
207a	Oct. "	Arnot Forest, N.Y.	Hl., Y.B., Be.	F (0-3)	83	4.4	160	1.65	9.43	2.00
207b	" "	" "	" "	H (3-6)	40	5.0	310	1.08	1.80	2.70
213F	Nov. "	Willett, N.Y.	Hl., Y.B., Be., Bass.	F 0-3	79	3.9 D	590	.75	3.54	.95
213H	" "	" "	" "	H 3-8	74	3.4 D	26	.42	1.63	.57
334F	July '30	Newcomb, N.Y.	Y.B., Be., S.M.	F 0-4	91	4.9	440	1.03	11.0	1.14
334H	" "	" "	" "	H 4-9	85	3.4	22	.62	4.20	.72
335F	" "	" "	" "	F 0-2	93	4.7	73	.90	12.3	.97
335H	" "	" "	" "	H 2-8	67	3.8	88	.17	.5	.25
336F	" "	" "	" "	F 0-3	89	5.5	2520	1.81	17.1	2.03
336H	" "	" "	" "	H 3-6	56	4.2	668	.66	1.5	1.19
337F	" "	" "	" "	F 0-2	91	5.1	1988	1.74	18.5	1.92
337H	" "	" "	" "	H 2-11	85	3.6	40	.64	4.3	.76
340F	" "	" "	Be., Y.B., S.M.	F 0-6	93	4.8	278	1.11	15.2	1.20
340H	" "	" "	" "	H 6-12	92	3.7	0	.67	8.2	.73
194a	Sept. '29	Saranac Lake N.Y.	Be., S.M., Y.B.	F 0-5	86	4.0	610	1.04	7.5	1.21
194b	" "	" "	" "	H 5-10	52	3.6	130	.43	.89	.84

Leaf duff

TABLE X. Greasy Duff

Sample no.	Date of sampling	Location	Stand	Layer, depth in cm.	Loss on ignition %	† pH	Nitrification in 3 months* mg. N/kg. "humus"	Total CaO		
								Per cent of dry soil	Per cent of aah	Per cent of "humus"
189Iva	Sept. '29	Crawford, N.H.	Y.B., Ba., R.S.	F 3-8	79	3.7	0	.57	2.7	.72
189IVb	" "	" "	" "	H 10-14	87	"	"	.53	4.1	.61
119	May '29	Waterville, N.H.	R.S.	F 1-7	93	3.5	590	.51	7.6	.55
120	" "	" "	" "	H 10-20	92	3.7	0 IV	.25	3.1	.27
121	" "	" "	" "	H 23-35	90	3.1	0 IV	.010	.1	.011
327F	June '30	Ampersand, N.Y.	R.S., Ba.	F 0-3	94	3.8	30	.42	7.4	.45
327H1	" "	" "	" "	H 3-11	79	3.2	60	4.04	9.7	.58
327H2	" "	" "	" "	H 11-15	36	3.3	140	4.32	6.7	12.12
328F	" "	" "	Y.B., S.M., Hl.	F 0-3	91	5.1	1600	1.43	16.4	1.56
328H	" "	" "	" "	H 3-12	72	3.3	20	.60	2.1	.84
317a	May '30	Blue Ridge, N.Y.	R.S., Ba., W.B.	F 0-10	94	3.3	0	.77	12.7	.82
317b	" "	" "	" "	H 10-20	97	2.8	0	.76	23.1	.79
317c	" "	" "	" "	H 20-30	96	2.9	0	.66	15.7	.69
317d	" "	" "	" "	H 30-53	93	3.0	0	.34	5.0	.37
325F	June '30	Eaton Lake, N.Y.	Y.B., R.S., Hl.	F 0-2	92	5.1	1600	.105	1.3	.115
325H1	" "	" "	" "	H 2-7	92	3.2	20	0	0	0
325H2	" "	" "	" "	H 7-13	86	3.0	25	.029	.2	.034
216	Jan. '30	Ellis Hollow, N.Y.	Hl., Y.B., Be.	H (3-5)	60	3.6 D	0	.70	1.74	1.17
217	" "	" "	" "	H (5-8)	73	3.5 D	0	.64	2.38	.88
218	" "	" "	" "	H (8-12)	85	3.1 D	0	.74	5.10	.87
330F	June '30	Johns Brook, N.Y.	R.S., S.M., Y.B.	F 0-3	93	4.8	60	1.75	25.8	1.88
330H1	" "	" "	" "	H 3-14	92	3.9	20	1.75	21.1	1.91
330H2	" "	" "	" "	H 14-22	31	4.2	80	2.01	2.9	6.55
350F	Aug. '30	Mohegan Lake, N.Y.	R.S., Be., Y.B.	F 0-3	92	4.0	280	.008	.1	.009
350H1	" "	" "	" "	H 3-10	90	3.0	68	—	—	—
350H2	" "	" "	" "	H 10-16	75	3.0	162	.025	.1	.034
362F	Sept. '30	Nehasane, N.Y.	Hl., Y.B., Be.	F 0-2	89	4.1	1720	1.01	9.0	1.14
362H	" "	" "	" "	H 2-5	88	3.1	31	.52	4.2	.59
363F	" "	" "	R.S., S.M., Y.B.	F 0-2	88	4.5	1060	.51	4.3	.58
363H1	" "	" "	" "	H 2-9	92	3.0	130	.36	4.3	.39
363H2	" "	" "	" "	H 9-12	90	2.9	40	.010	.1	.011
341F	July '30	Newcomb, N.Y.	R.M., S.M., Y.B.	F 0-1	92	4.6	89	.81	10.2	.87
341H	" "	" "	" "	H 1-5	53	4.0	51	.047	.1	.088

* IV = Nitrification in 4 months.

† D = pH determined on dried sample.

TABLE X.—Continued

Sample no.	Date of sampling	Location	Stand	Layer, depth in cm.	Loss on ignition, %	† pH	Nitrification in 3 months* "humus"	Total CaO		
								Per cent of dry soil	Per cent of ash	Per cent of "humus"
342F	July '30	Newcomb, N.Y.	R.S., Hl., Be.	F 0-3	92	5.2	1000	1.43	17.8	1.55
342H1	" "	" "	" "	H 3-11	93	3.5	0	.47	6.5	.51
342H2	" "	" "	" "	H 11-18	92	3.2	0	.33	3.9	.36
343F	" "	" "	R.S., Hl., Ba.	F 0-2	93	5.0	1294	1.43	19.6	1.54
343H1	" "	" "	" "	H 2-14	94	3.1	42	.25	4.4	.26
343H2	" "	" "	" "	H 14-22	91	3.0	52	.064	.7	.071
344F	Aug. '30	" "	Y.B., S.M., Be.	F 0-5	91	5.0	1300	1.31	14.6	1.45
344H	" "	" "	" "	H 5-12	44	4.0	300	.056	.1	.13
359F	Sept. '30	" "	Be., R.S., Ba.,	F 0-2	91	4.4	760	.99	11.2	1.08
359H1	" "	" "	" "	H 2-6	93	3.0	90	.17	2.3	.18
359H2	" "	" "	" "	H 6-12	85	3.1	—54	.029	.2	.034
322F	June '30	Pack Forest, N.Y.	Hl., R.S.	F 6-2	88	4.3	150	.036	.3	.041
322H	" "	" "	" "	H 2-6	57	4.2	60	.95	2.2	1.67
351F	Aug. '30	Racquette Lake, N.Y.	R.S., Ba., Y.B.	F 0-3	93	4.0	750	.52	7.7	.56
351H1	" "	" "	" "	H 3-14	90	3.0	60	.22	5.0	.23
351H2	" "	" "	" "	H 14-17	75	2.9	45	.049	.2	.065
352F	" "	" "	R.S., Y.B., Ba.	F 0-4	95	4.1	50	.47	9.6	.49
352H	" "	" "	" "	H 4-13	92	3.1	60	—	—	—
333F	July '30	Sabbatis Mt., N.Y.	R.S., Y.B., W.B.	F 0-2	94	3.9	70	.40	6.8	.43
333H	" "	" "	" "	H 2-17	85	2.9	40	.20	1.3	.23
215F	Nov. '29	Smithville Flats, N.Y.	Hl., Y.B.	F 0-1	94	3.6 D	0	.78	13.3	.83
215H	" "	" "	" "	H 1-12	92	2.9 D	130	.49	5.76	.54
195a	Sept. '29	Tupper Lake, N.Y.	Be., S.M., Y.B.	F 0-3	80	4.2	1160	.43	2.10	.54
195b	" "	" "	" "	H 3-10	73	3.4	180	.84	3.12	1.15
196a	" "	Wanakona, N.Y.	R.S., Hl., Y.B.	F 0-4	90	3.9	550	.74	7.05	.83
196b	" "	" "	" "	H 4-14	82	3.4	150	.81	4.60	.98
170	July '29	Allan Seeger Mon., Pa.	Hl., Y.B.	F 0-3	—	—	10	—	—	—
171	" "	" "	" "	H 5-10	92	3.2 D	13	.86	11.0	.93
172	" "	" "	" "	H 10-20	83	3.2 D	—17	.70	4.1	.84
173	" "	Hearts Content, Pa.	" "	F (0-3)	88	3.6 D	22	.56	4.5	.64
174	" "	" "	" "	H (3-10)	93	3.3 D	—42	.49	6.7	.54
175	" "	" "	" "	F 0-2	92	3.4 D	7	.01	.1	.01
176	" "	" "	" "	H 3-7	94	2.9 D	—5	.22	3.9	.23
177	" "	" "	" "	H 7-12	95	2.9 D	—2	.16	3.1	.16
178	" "	" "	" "	F (0-3)	68	3.4 D	—15	.03	.1	.05
179	" "	" "	" "	H (3-10)	86	2.9 D	—26	.01	.1	.02

TABLE XI. *Fibrous Duff*

Sample no.	Date of sampling	Location	Stand	Layer, depth in cm.	Loss on ignition, %	pH	Nitrification in 3 months ing. N/kg. "humus"	Total CaO		
								Per cent of dry soil	Per cent of ash	Per cent of "humus"
316a	May '30	Blue Ridge, N.Y.	R.S., Ba., W.B.	F 0-14	95	3.5	0	.64	12.1	.68
316b	" "	" "	" "	H 14-28	88	3.4	195	.012	.1	.014
349F	Aug. '30	Mohegan Lake, N.Y.	R.S., S.M., Y.B., Ba.	F 0-4	91	4.0	300	.03	.1	.009
349H	" "	" "	" "	H 4-10	62	3.4	200	.031	.1	.044
356F	June '30	Mt. Kempshall, N.Y.	R.S., W.B.	F 0-2	94	3.9	50	0	0	0
356H	" "	" "	" "	H 2-6	74	3.3	50	0	0	0
360F	Sept. '30	Nehasane, N.Y.	Y.B., R.S., S.M., R.M.	F 0-3	92	4.0	-26	.40	5.1	.44
360H	" "	" "	" "	H 3-11	91	2.9	-20	.009	.1	.010
357F	" "	Newcomb, N.Y.	R.M., Ba., R.S., Hl.	F 0-3	92	4.8	-27	1.17	15.0	1.27
357H	" "	" "	" "	H 3-19	94	3.5	160	.25	4.5	.27
364F	" "	" "	Hl., R.S., Ba., R.M.	F 0-3	94	3.7	-9	.95	14.8	1.01
364H1	" "	" "	" "	H 3-31	96	3.1	-10	.68	15.8	.71
364H2	" "	" "	" "	H 31-39	94	2.9	-10	.006	.1	.007
355F	Oct. '30	" "	R.S., Hl., Ba., R.M.	F 0-3	95	3.9	10	.73	13.5	.77
355H	" "	" "	" "	H 3-24	95	2.3	0	.53	9.8	.56
308a	May '30	Pack Forest, N.Y.	W.P., Hl.	F 0-3	93	4.0 D	0	.31	7.8	.35
308b	" "	" "	" "	F 3-6	93	3.6 D	0	.55	8.1	.59
308c	" "	" "	" "	H 6-8	86	3.4 D	0	.56	4.1	.65
347F	Aug. '30	Sagamore, N.Y.	R.S., Ba.	F 0-1	93	4.4	213	.73	10.2	.79
347H	" "	" "	" "	H 1-12	85	3.1	100	.060	.4	.071
348F	" "	" "	Pop., W.P., Ba.	F 0-5	90	4.3	160	.83	8.5	.92
348H	" "	" "	" "	H 5-13	52	3.7	90	.048	.1	.090
338F	July '30	Waterbarrel Mt., N.Y.	R.S., Ba., W.B., Y.B.	F 0-2	92	3.9	440	.39	5.0	.42
338H	" "	" "	" "	H 2-9	75	3.2	200	.36	1.4	.48
329F	June '30	Whiteface Mt., N.Y.	Alpine, Vac. <i>uliginosum</i> Ba., Vac. <i>uliginosum</i>	F 0-4	41	3.6	240	2.61	4.4	6.41
329H	" "	" "	" "	" "	" "	" "	" "	" "	" "	" "
159	July '29	Superior Nat. For., Minn.	Ba., W.S.	H 4-24	46	3.8	150	2.005	3.7	4.38
160	" "	" "	" "	F 0-5	85	4.2	0	—	—	—
	" "	" "	" "	H 5-8	62	4.1	0	—	—	—

D = pH determined on dried sample.

Johnson, Department of Zoology, New York State College of Forestry, for determinations of earthworms and to Prof. K. M. Wiegand of Cornell University for determination of some plants. Most of the plants have been determined by the authors or by Mr. C. Heimburger. Mr. F. B. Howe, New York State Soil Surveyor, has kindly inspected and classified a couple of our profiles in the field.

Explanation of Tables VII to XI

Alder	<i>Alnus incana</i>
Ba.	Balsam Fir, <i>Abies balsamea</i>
Bass.	Basswood, <i>Tilia americana</i>
Be.	Beech, <i>Fagus grandifolia</i>
Bl.Ch.	Black Cherry, <i>Prunus serotina</i>
Elm	Elm, <i>Ulmus americana</i>
Hb.	Hop Hornbeam, <i>Ostrya virginiana</i>
Hi.	Hickory, <i>Carya ovata</i> and <i>cordiformis</i>
Hi.	Hemlock, <i>Tsuga canadensis</i>
Pop.	Poplar, <i>Populus grandidentata</i> and <i>tremuloides</i>
R.M.	Red Maple, <i>Acer rubrum</i>
R.O.	Red Oak, <i>Quercus rubra</i>
R.S.	Red Spruce, <i>Picea rubra</i>
S.M.	Sugar Maple, <i>Acer saccharum</i>
W.A.	White Ash, <i>Fraxinus americana</i>
W.B.	White Birch, <i>Betula papyrifera</i>
W.O.	White Oak, <i>Quercus alba</i>
W.P.	White Pine, <i>Pinus Strobus</i>
W.S.	White Spruce, <i>Picea canadensis</i>
Y.B.	Yellow Birch, <i>Betula lutea</i>
IV	Nitrification in 4 months
D	pH determined on dried sample

The indications under "Stand" are not complete lists. The order of importance of constituents is roughly indicated by their sequence in the enumeration.

Depth figures in brackets are approximate.

Summary

A review is given of earlier efforts on the problem of classifying forest humus layers. The earlier proposals are critically discussed. A scheme is proposed to fit conditions in the northeastern United States.

The authors retain P. E. Müller's two main groups, and follow the Scandinavian school in defining the *mull* group morphologically. Specific types listed are *crumb mull*, *grain mull*, *twin mull*, and *detritus mull*. For the other main group, the word *duff* is proposed in English. Specific types listed are *root duff*, *leaf duff*, *greasy duff*, and *fibrous duff*.

The distribution of the more important types within the region is outlined. Ground water conditions, lime content and texture of the soil seem to be particularly important factors in locally determining the type of humus layer, just as has been found to be the case in Europe.

Some plants are listed as indicators of mull and of duff. The most valuable hardwood species of the region seem to be among the mull preferring plants.

Storage and inoculation tests have shown nitrification to occur in all types of forest humus layer distinguished within the region, thus to be much more widespread than could be expected from European experience. Still, there is a great difference between various types, the mull samples being practically all nitrifying, whereas the majority of samples of pronounced duffs (greasy and fibrous duff) did not nitrify. Storage tests yielded surprisingly low values for crumb mull as compared with less pronounced mulls and root duff. Inoculation tests agreed better with the expectation from previous experience and the character of the vegetation. The discrepancies are ascribed to a "sampling effect" to be discussed in a later paper.

The pH range of nitrifying samples has been found to be extraordinarily wide, down to pH 2.9, which seems to be lower than the lowest value hitherto on record. The minimum pH found in the whole material being 2.8 (and this only in one sample), it seems unlikely that the acidity in itself is the inhibiting factor where nitrification does not occur. Still there is within the duff group, all over the range represented, a clear positive correlation between pH of sample and intensity of nitrification during storage. Within the mull group, the correlation is doubtful. For the whole material available, taken together, the inoculation tests show a positive correlation between pH and nitrification all over the range represented, but the storage tests seem to indicate an optimum at pH 5-6. The latter is explained as a statistical freak due to group differences within the material.

The average pH of the types decreases all the way from crumb mull to greasy and fibrous duff.

In the duffs, a striking difference in lime content between F- and H-layers is frequently noted. This is taken as an evidence both of the "lime-pumping" action of the stand and of the rapid leaching out of lime under the given conditions.

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REVIEWS

GEOGRAPHY OF AMERICAN NOTABLES¹

The most important problem of human ecology is to determine exactly how far the presence of different types of people in any given region depends on physical environment as compared with social environment and heredity. In his "Geography of American Notables," Professor Visser has made a most interesting and valuable attempt to solve this problem in respect to persons of unusual ability in the United States. With the utmost care and patience he has gathered a vast body of facts about all sorts of leaders. His main subject of study has been nearly 1,800 scientists whose names are starred in Cattell's "American Men of Science." The stars mean that these men are regarded by their colleagues as the more eminent leaders in their respective lines.

Having ascertained where these leaders were born, Visser compares the distribution of their birthplaces with that of many other more or less eminent people. Long and valuable tables give data as to members of the most exclusive scientific, artistic and literary organizations, as to leading authors, educators, engineers, labor leaders, farm leaders, and millionaires, and as to the 9,000 unstarred scientists and the 24,000 people in "Who's Who."

This leads Visser to his first conclusion, a conclusion which seems unsailable: In a general way all types of preeminence show the same geographic distribution. Leaders are born mainly in the northern part of the United States, but not in the extreme north. Southern New England has been supreme in this respect. It still stands at the top, although the regions farther west and on the Pacific coast are rapidly gaining on it. Southward from the main belt where leaders are born, there is a steady and marked decline. Northward, such regions as northern New England, the northern parts of Michigan, Wisconsin, and Minnesota and North Dakota also show a slight decline. In the west an area of decline is found in the Rocky Mountains, but a noteworthy recovery occurs on the Pacific coast. This conclusion is not new, but Visser greatly strengthens it.

His next aim is to compare the distribution of the birthplaces of leaders with the distribution of other measures of social merit. Accordingly he presents us with another array of tables and maps showing data as to army intelligence tests, the circulation of magazines, both popular and "highbrow," crime, venereal disease, income, education, intelligence as shown by the ac-

¹ Visser, S. S., *Geography of American notables: A statistical study of birthplaces, training, distribution: An effort to evaluate various environmental factors. Indiana University Studies, Vol. 15, Study No. 79, pp. 1-138, June, 1928.*

curacy of age statistics in census returns, health, transportation facilities, and percentages of persons engaged in the professions and in manufacturing.

From all this Visher draws a second well founded conclusion, namely that the distribution of practically all reliable measures of social merit is in general essentially the same as that of leadership. Here he pauses long enough to point out that the southward decline of productivity in leaders and in other evidences of social progress is in accord with the conditions of climate. He does not recognize, however, that the incipient northward decline and the decline in the Rocky Mountains are also exactly what would be expected on the basis of the effect of long cold winters and great aridity upon health and activity.

Visher's next object of study is local variations in the production of leaders. Here he is at his best, and makes a really important contribution to our knowledge of mankind. Taking his own state of Indiana and the five adjacent states he examines the birthplaces of his scientists and other leaders. He shows that there are many great local variations which at first might seem highly erratic, but which are in reality almost entirely explicable on the basis of selective migration. These variations join with other facts in demonstrating that in proportion to their numbers the rural population and the manufacturing population of cities furnish very few leaders. The places where leaders are born in large numbers in comparison with the total population are the better sections of cities, the towns, especially the county seats, and above all college towns and the choice suburbs of great cities. Moreover, it is from the homes of the professional classes, and especially those of the ministers of the more liberal denominations, that the yield of eminent leaders is proportionally greatest. Other factors, such as poor soil, poverty, isolation, or the presence of unpleasant occupations, such as mining or manufacturing, do indeed diminish the proportion of leaders, but these are minor incidents.

The great outstanding fact is that, in proportion to the population, leaders are born in greatest numbers in places where favorable circumstances, or even accidents, have concentrated an unusual number of highly intelligent people. But the accidents are the exception. In general the able people are attracted to certain places because those places offer advantages. Such people are mobile. They are well informed and therefore know whether they are well located. They have means wherewith to move, or at least the vigor and skill to change their places of residence when they see reason to do so.

Thus certain types of able people become concentrated in certain regions. The location of those regions may be determined by climate, soil, the relief of the land, routes of transportation, proximity to old homes, routes of transportation, the accidental location of colleges, or any one of hundreds of other factors. The people who choose these regions as homes may be Puritans, Quakers, Scotch-Irish Presbyterians, Germans who seek political liberty, missionaries, educators, or successful business men. The essential fact is that selected groups of more than average ability settle in certain

regions and reproduce themselves, while other groups of less ability settle elsewhere.

Then Visser tries to determine whether the presence of educational facilities has much to do with the distribution of leadership. This section of his work is not so well knit as the rest, but it is interesting because of the abundant data whereby we may compare the efficiency and reputation of the universities in which we happen to be interested. Visser's conclusion is that the mere presence of educational facilities has little to do with the development of leadership. Otherwise why should Maine, with no real university when the present leaders were growing up, supply far more leaders in proportion to its population than Maryland, with Johns Hopkins in its midst? Because the young men of Maine are born with the mentality for leadership, and perhaps because they are well trained at home, they find opportunities for the best education, even if they have to go to Baltimore.

This leads Visser to his final conclusions. The two most vital and debatable of these are as follows: 1. "The yield of notables in proportion to population does not depend primarily upon climate, soil, or other resources, or upon the density of population or upon the presence of educational facilities, or upon the stage of settlement. 2. The yield of notables depends chiefly upon the characteristics of the population, especially upon their ideals" (page 136). The character of the predominant population changes with migrations, differential birth-rates, and with comparative opportunities for individual advancement.

It seems to me that these conclusions do not quite express the full meaning of the scholarly discussion which precedes them. They imply that either environment or biological and social inheritance must be the dominating factor in determining the distribution of leadership. Visser gives admirable reasons for believing that biological and social inheritance are the primary reasons for certain local differences between one part of a state and another, although even there the differences owe their exact location to the geographic environment. On the other hand, he gives no evidence whatever to show that the steady southward decline from the zone where most leaders are produced is due to anything except the direct or indirect effects of climate. The real conclusion to which we are led by this admirable paper would seem rather to be something like this: The distribution of leadership over the United States is due to a complex interplay of physical environment, biological inheritance, and social inheritance. These three are as inseparable and as necessary to the production of leadership as food, drink and air to the maintenance of life. Nevertheless, as we survey the ever-growing body of facts we see more and more clearly that in the broadest relationships climate is of especial importance; in the more local distribution of centers of leadership the biological and social factors assume greater significance.

ELLSWORTH HUNTINGTON

VERTEBRATE NATURAL HISTORY OF A SECTION OF NORTHERN CALIFORNIA
THROUGH THE LASSEN PEAK REGION¹

Joseph Grinnell and his associates have been busy for many years gathering and placing on record information concerning the animal life of the Pacific Coast region of North America with particular reference to California. In this single state one may find primary and man-made animal communities widely differing in taxonomic and physiological characteristics in close juxtaposition where they invite comparisons and contrasts. The present study was restricted to a strip of territory of 24×124 miles in northern California which contains such contrasting topographic features as the Sacramento River valley floor at 300 feet elevation, Lassen Peak, 10,451 feet, and the Great Basin platform at 5,300 feet, and also includes Eagle Lake, the largest lake of the northern California region. The study was restricted to the vertebrate life, largely to the land vertebrates, in the hope of gaining more insight than would be possible in the time available if the whole biota were surveyed. The present bulky report does not repeat previously published matter, and is addressed to the serious student.

The authors state that in preparing the report they have had the following objectives in mind: "What species and subspecies of land vertebrates are present within the section arbitrarily outlined? What is the relative abundance and the local distribution of each? What factors determine the presence and habitat distribution, and the annual cycle of activity of each?" Further, they aim to present "the definition of a way to analyze vertebrate communities and successions."

In connection with the last objective, it is interesting to note that "no instruments have been employed in our study of the environment of this section, first because it is not known what kinds of factors are of most importance in determining the presence or absence of the types of animals we are studying. Some biotic or physiographic influences (not now measurable) may have more importance for the distribution of a particular animal species than any of the physical factors capable of being expressed in quantitative form." A water-killed "stub-forest" which supplies nesting sites is given (p. 47) as an example of a single factor which is not readily measurable that operates to determine the presence of certain species of birds. As a second reason for not attempting physical measurements, attention is called to lack of time for measuring factors of possible significance, such as light, moisture, air movement and heat. Hytherographs from three stations are given, and one page is devoted to the general discussion of the climate. It appears that the rainfall at one place near the section studied ranges from a mean of 27 inches in January to less than one inch in July

¹ Grinnell, Joseph, Dixon, Joseph, and Linsdale, Jean M. Vertebrate natural history of a section of northern California through the Lassen Peak region. *University of California Press*. v + 594 pp., 181 text figures, 1930.

or August, while at the same point the monthly mean temperatures range from 35 to 65° F.

Little use is made of such information in studying the animal life, and the general factors accounting for the habitat limitations of terrestrial vertebrates as recognized in the Lassen section were:

"1. The inherent structural and instinctive peculiarities of each species in question.

"2. Vegetation as it provides the requisite type of breeding place, forage place, food, and shelter for each species.

"3. Nature of ground or rock surface as providing requisite type of breeding place, forage place, and shelter for each species.

"4. Presence of water and manner of its availability to each kind of animal.

"5. Altitude in its influence upon (aside from '2,' '3,' and '4') such conditions as warmth² and moisture² of the atmosphere and terrain.

² Unmeasured.

"6. Physiographic relationships of the section with surrounding territories, near and far, as affecting or modifying the other factors.

"7. Presence or absence of other animals whose activities or numbers critically affect the food supply, individual safety, or shelter of each species in question."

A suggested list of the habitats which would repay further study include the aquatic, low vegetation, brush land, woodland, forest land, rock land, and man-made, each of which is further subdivided on the basis of its outstanding plant or physiographic or other features. Some 70 pages, profusely illustrated by habitat photographs, are devoted to the discussion of the land vertebrate life of these habitats, but without undertaking to list more than the characteristic animals in each. The animal life is further analyzed in terms of Merriam's life-zones as mapped by the distribution of conspicuous plants used as zone-indicators; life-zone check lists are given with care according to the breeding range of the vertebrate inhabitants.

A noteworthy aspect of this phase of the study is that "the northward extension of the Lower Sonoran life-zone in the upper Sacramento Valley marks a more northern position of that zone (a little above the 40th parallel) than has been reported from any other place across the North American continent." This extension is interpreted as being due to the warm temperatures brought into the region by the low Sacramento Valley. The Boreal life-zones are less extensive in the section studied than are the Austral, and the animals of the two sets of zones show a 1:2.5 ratio. This is in accordance with the so-called "law" of small areas, and with the fact that "there are more and more diverse ecologic niches included in the Austral portions of the territory." Niches are defined here as "subsistence affording units of occupancy for vertebrate species."

The faunal relations are further analyzed by means of lists and 37 strip

locality maps in terms of faunal areas with particular reference to the Great Basin, Californian, Cascade and Sierra Nevadan faunae.

Population estimates and areal censuses of birds indicate that on account of the concentration of numbers of birds in favorable areas, the total population for the Lassen Peak section is brought up to or near the mean figures for the whole United States of two birds per acre in the nesting season. The Lower Sonoran life-zone, containing the riparian tracts along the Sacramento River "where maximum warmth and moisture are both present" (both unmeasured), was richest in bird life in summer, the Canadian life-zone was next, while the Arctic-Alpine Zone is a blank except for vagrants.

The remaining sections of the report give a vertebrate check-list followed by "general accounts" of the local occurrence of each form listed. With the aid of these notes, any one interested could fill out habitat lists in detail.

In all, 3,592 specimens were collected in the 673 field-days upon which the report is based.

As natural history, which is all the title claims, this is excellent, basic material well worth preserving in the form in which it is presented. It is unfortunate that facilities for publication at such length are not available to all workers who have the will and the wit for making comparable observations. I should personally like to know the extent to which physical or biotic factors measurable by modern methods are correlated with such vertebrate distributions as are described in this study; the numbers of vertebrates other than birds present in the different major environments or in habitat niches; and the discoverable relations between invertebrate and the vertebrate elements of these biotic communities. Even so, it is no criticism of these workers that they have not been able to collect all these data for this present report.

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NOTES AND COMMENT

EXPOSED COMBS OF THE HONEY BEE

Bee-trees have always been the Pandora's box of the primeval forests, furnishing joy and excitement for bears and pioneers alike. But they, like other features of wild life, are disappearing before the march of civilization. With the felling of the trees for the making of fields and subdivisions, and with the advent of modern tree-surgery, hollow trees suitable for the refuge of swarming honey-bees about St. Louis are becoming few. These homeless swarms of bees are in a pathetic plight.



FIG. 1. Nest of honey-bees attached to a limb, exposed and unsheltered. Found near St. Louis, Missouri

During the past few years I have seen about the suburbs of St. Louis 8 combs of honey-bees attached exposed and unsheltered to the limbs of trees. These have been of various sizes, from the size of a pair of human hands to the size of the nest figured herewith (Fig. 1).

This beautiful specimen was found attached to a small tree in the Mississippi bottom-land near Wicks, Missouri, and was made by the bees in 1929. It had become so heavy that the limb to which it was attached was bent nearly to the ground. The colony of bees had withstood wind and rain in the open sufficiently well to construct this comb, and filled it with larvae and honey, but they, like all of the other colonies seen in such open places, could not withstand the winter in the open, and, when the comb was found in the spring, several thousand dead bees were seen in the crevices, showing at least that they had clung on to the very last and would not desert the nest.

The building of combs in the open tree-tops is not new to the honey-bee tribe. This method is merely a return to a vestigial instinct of nidification, brought to life again by the lack of hollow trees in which to build their combs. Wheeler¹ says that the form and position of the combs of our honey-bee, when suspended in the open, are much like those of *Apis dorsata* and *Apis florea* in southern Asia where the honey-bee lived before it was domesticated and exported to temperate regions, and "that we are justified in interpreting this unusual method of nidification as a return to ancestral conditions; in other words, as a revival of a lingering or a vestigial instinct, called forth by some unusual stimulus, such as the inability to find a suitable nesting cavity at the proper time and in the proper place. The manifestations of this instinct in temperature regions is worse than purposeless, for it leads to the extinction of the colony on the approach of winter."

A similar comb, built among the wisteria vines on the grounds of the Missouri Botanical Garden, at St. Louis, is described in the Bulletin of the Missouri Botanic Garden, 15: 163. 1927.

PHIL RAU

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A FIFTEEN YEAR GROWTH RECORD IN FRESH-WATER MUSSELS

In June, 1910, the writer undertook a study of the rate of growth and migration of fresh-water mussels. About 900 specimens were tagged, weighed and measured and placed back into the streams to be later reclaimed and checked. The reclaiming and checking was successfully carried out in September, 1910, June, 1911, and September, 1911.

As the investigation was satisfactorily completed,¹ and the writer moved away from the vicinity, no further attention was given to these tagged specimens. However, in August, 1925, an opportunity was afforded to re-visit the Shoofly Creek site where some of the tagged mussels had been placed. It was found that the stream bed had markedly changed during the fifteen years, 1910-25. What was formerly a ponded stretch with water from 2 to 6 feet in depth in various parts of the stream, had been transformed into a gravel-choked stream floor with a much lower water level.

The experimental site, Shoofly Creek, is briefly described (Isely, 1913, p. 7) as follows:

"Shoofly Creek is a tributary of the Chikaskia. In very dry weather the water stops flowing over the shallow, gravelly stretches; but the ponded sections often a mile in length and with water 2 to 6 feet deep, have a constant water supply. In certain of these ponded portions mussels are fairly abundant."

¹ *Am. Journ. Psychol.*, 19: 4. 1908.

¹ Isely, F. B., *Experimental study of the growth and migration of fresh-water Mussels. Appendix III. Rept. U. S. Com. of Fish.*, 24 p., 3 pls. 1913.

In 1910, mussels were abundant in this particular stretch of Shoofly Creek. In 1925 only a remnant of the former abundant numbers was left. After a short time spent in collecting by a party of three, a lot of about 50 specimens was secured. Three of these, all belonging to the species *Quadrula undulata* (*Amplema costata*² Raf.) were found to be tagged individuals that had been originally planted in 1910.

The 1910 and 1925 measurements of the 3 reclaimed mussels are compared below under their respective numbers:

Specimen 72—This specimen carries the following description in the field notebook record for June 14, 1910: weight—185 grams; length—93 mm.; height—61 mm.

For August, 1925, or 15 years later, the measurements are as follows (see Fig. 1): weight—310 grams; length—115 mm.; height—82 mm.

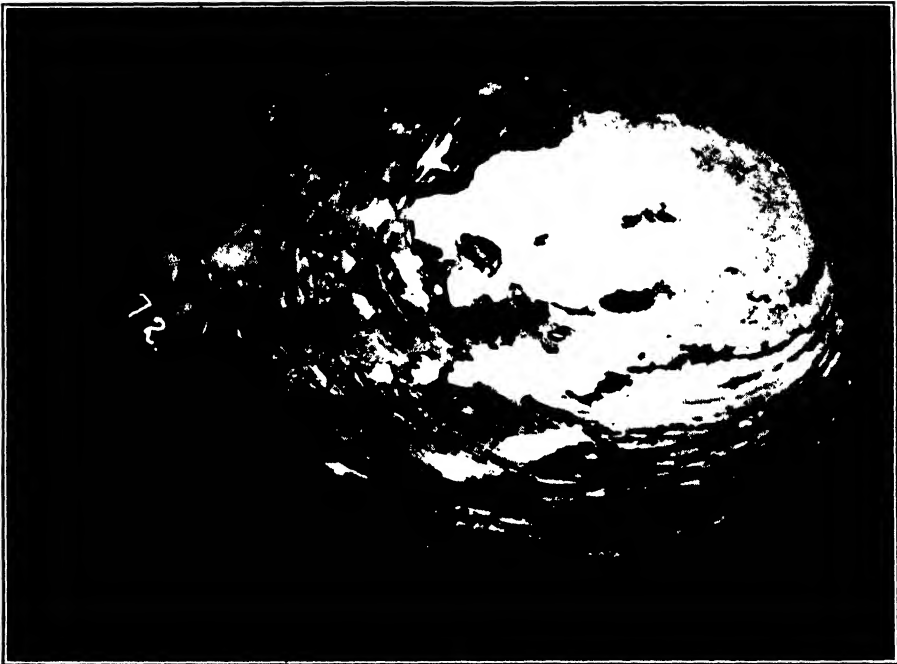


FIG. 1. Photograph of specimen No. 72, *Quadrula undulata*, showing 15 years of growth. Approximately natural size

This specimen belonged to the group of mussels that is designated in my 1914 paper, page 7, as "Lot A."

"Lot A" specimens are described as follows:

"Shoofly, lot A, 140 specimens—Nearly all of these were *Quadrula undulata* (three-ridge) and were taken from the direct site where they were planted after tagging. All of the *Q. undulata* (three-ridge) secured in the Shoofly were large; out of some 500 specimens handled in two days, only 4 weighed under 200 grams."

This would indicate that specimen No. 72 was one of the smallest mussels from the original Lot A.

Specimen 297—As already indicated, the fresh-water mussels in the Shoofly Creek

² Isely, F. B., The fresh-water mussels fauna of Eastern Oklahoma, *Proc. Okla. Acad. of Sc.*, 4: 43-118, 1925.

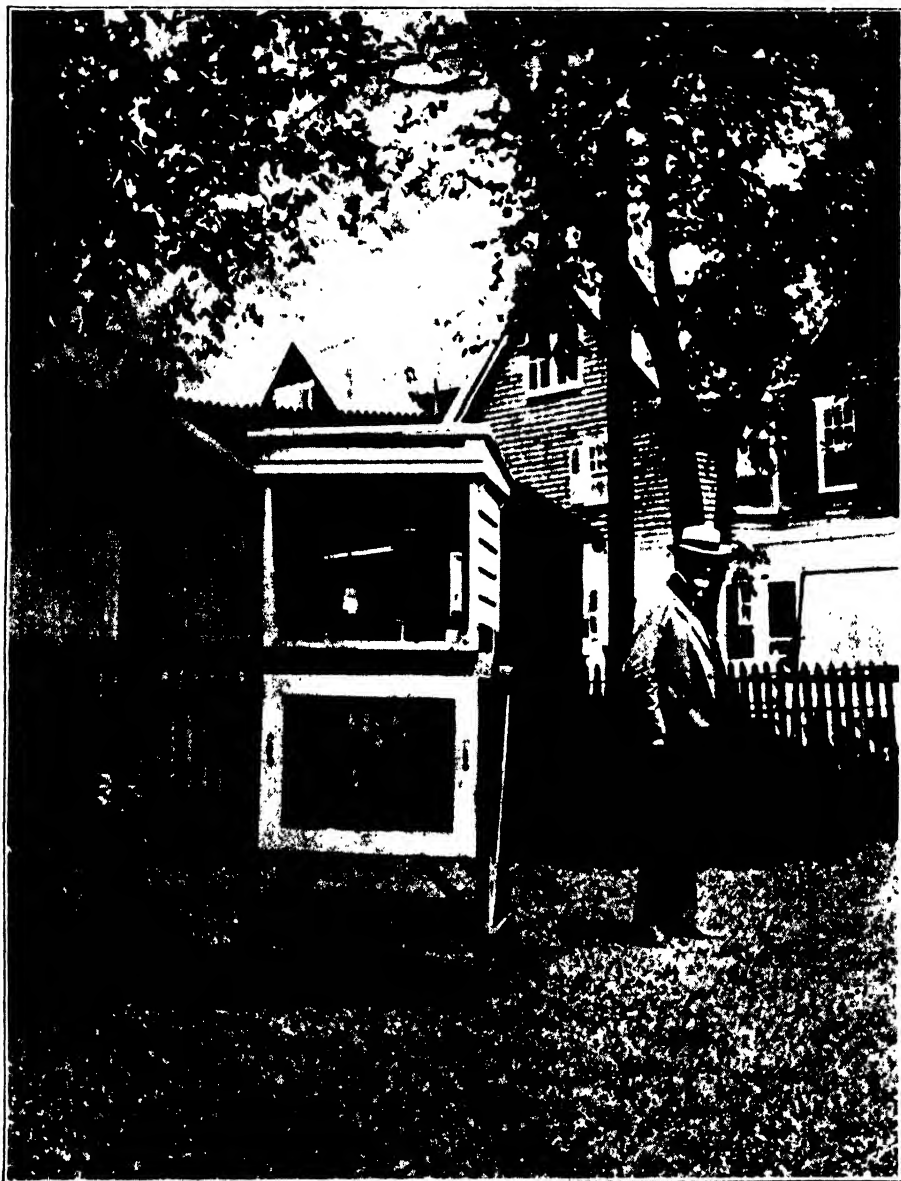


FIG. 1. Thermometer shelter $30 \times 24 \times 24$ inches inside measurement. Note distance of thermometers from roof and sides

in 1910 were almost all full grown. Practically no young mussels were found. In order to secure younger mussels for the growth study, 168 mussels had been carefully collected from the Chikaskia River. These were weighed, measured and tagged, and planted in the Shoofly. Specimen 297 belongs to the transplanted group, and is shown in the record (Isely, 1913, p. 8) as one of the "Lot D" specimens.

There is no weight record in the field notes for Specimen 297, but length and height figures are as follows: In June, 1910: length—82 mm.; height—54 mm.

In August, 1925: length—117 mm.; height—78 mm.

The third specimen in our series has lost the tag, but the copper wire which had supported the tag is still clearly intact. Although there is no back record by which it may be checked, present measurements indicate that it was 98 mm. long at the time of tagging.

For June, 1910, we find the measurements as follows: length—98 mm.; height—64 mm.

For August, 1925, the measurements are: length—127 mm.; height—86 mm.

Summarizing, it will be observed that these recovered mussels show an average increase in length for the 15 years since they were tagged of nearly 2 millimeters per year. This average is higher than the average given in connection with Tables 6 and 7, page 14 in the former report. To be sure, only 3 specimens are involved in this average.

The former record was for one year, and shows the growth for 20 large mussels for June 1910 and June 1911. That record suggested that for mussels weighing over 200 grams the rate of growth or increase per year would be about one millimeter. These 3 specimens would suggest that that average is low. As these mussels were over 10 years old at the time of tagging, their present age may be placed as between 25 and 30 years.

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THERMOMETER SHELTERS

I was interested in the description and the illustration of the shelter used by Messrs. Chapman, Wall, Garlough and Schmidt in their paper in the April number of *Ecology*.¹ The problem of a suitable shelter for thermometric records is not always correctly solved, as I have found by experience. My first attempt in the matter led to a measurable error, for the reason that the shelter was too small. The accompanying cut (Fig. 1) shows the main features of the second. Its cubage is about 10 times that of the first; it is about 4 times that of the shelters used by the U. S. Weather Bureau.

It is an axiom of thermometry that air in the sun has the same temperature as in the shade. This is true of air in motion, but not of pocketed volumes of air. Hence, a well-louvered shelter theoretically may be set in the open where direct sunlight falls upon it during daylight hours. In practice, however, the shelter may become hot enough to radiate warmth to the inclosed thermometers. That was the case with my first shelter, and inaccurate temperature records resulted. So I built another $30 \times 24 \times 24$ inches approximately, inside dimensions (Fig. 1). The thermometers are placed at a distance of 1 foot from the walls; the thermograph rests on a stand 3 inches high. Sides and bottom are louvered, the front is a screen of course mesh. The roof is covered with thick linoleum.

For convenience of access it is placed about 6 feet from the south side of the house, a position open to objection; for, even with the protection of the shelter, in very hot

¹ Chapman, R. N., Wall, R., Garlough, L., and Schmidt, C. T. A comparison of temperatures in widely different environments of the same climatic area. *Ecology*, 12: 305-322, 1931.

weather enough heat is radiated from the building to the shelter to affect temperature readings. Where practicable, a shelter is best placed in the open and in the afternoon shade of a tree.

In my experience the virtue of a thermometer shelter depends chiefly on its cubage. The shelter illustrated on page 308² seems to be most admirably adapted to the service for which the authors of an interesting article are employing it. I am wondering, however, if the proximity of the roof-boards to the instrument does not permit the radiation of enough warmth to affect the records of the thermomograms. With my first shelter, the daily maxima in very hot weather were some times 2 degrees F. too high—the error depending largely on the clearness and the cleanness of the air. I am writing this for information and not in criticism.

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INTERNATIONAL HORTICULTURAL CONGRESS OF 1930¹

The Report and Proceedings of the International Horticultural Congress, which was held in London in 1930, contains, among many papers of interest to horticulturalists, several which will be welcomed by workers in plant ecology and physiology.

Barker² discusses the work at Long Ashton, England, on the influence of environmental factors on fruit trees. He devotes most attention to the soil, and to nutritional relations, showing the effects of deficiency in certain elements. For example, phosphorous deficiency was associated with poor shoot growth, late breaking of the buds in spring, a characteristic bronzing of the foliage, and early defoliation. He found a close relation between potassium and the water relations of the tree. A tree containing a relatively high amount of potash resists drought better than one containing a less amount, "and it would appear that potash in some way enables a plant to check excessive transpiration under drought conditions."

Denny³ gives a brief but pithy discussion of the external stimuli which break dormancy of buds. He gives examples of the inconsistent results of past experiments, which have shown that dormancy may be broken by either high or low temperature, by increased light or darkness, and by conditions of high or low oxygen supply. With chemical treatments we do not meet the inconsistencies, but have the difficulty of understanding why so many chemicals can produce approximately the same or similar results.

Reid⁴ discusses plant nutrition, particularly in connection with the carbohydrate-nitrogen ratio, showing that any condition which favors a high proportion of carbohydrate to nitrogen favors root development. Her experiments suggest that early fertilization with an abundance of readily available nitrogen does not favor the development of properly proportioned (roots to top) seedlings.

² *Loc. cit.*, footnote 1.

¹ International Committee for Horticultural Congresses. Report and Proceedings, International Horticultural Congress, London, 1930. The Royal Horticultural Society, Vincent Square, London, 1931.

Only a limited number of copies of the Report is available. It can be obtained from the Royal Horticultural Society, Vincent Square, Westminster, London S. W. 1, England, at 15 shillings, postpaid.

² Barker, B. T. P., The fruit tree complex in relation to environment. *Loc. cit.* footnote 1, pp. 325-331.

³ Denny, F. E., The excitation of buds under external stimulus. *Loc. cit.* footnote 1, pp. 77-82.

⁴ Reid, Mary E., The influence of nutritive conditions of seeds and cuttings upon the development of roots. *Loc. cit.* footnote 1, pp. 165-169.

Zimmerman ⁵ describes some interesting experiments on the relation of oxygen supply to the development of roots of cuttings of various plants in water. Analyses of the oxygen content showed that willow (*Salix pendula*) cuttings will form roots in water containing as little as 1 part per million of oxygen. English ivy (*Hedera helix*) formed roots with 4 p.p.m. Tomato (*Lycopersicum esculentum*) cuttings produce oxygen by photosynthesis under water. Eliminating the light by wrapping the cylinders in black paper caused the depletion of the oxygen and the disintegration of the cuttings.

Of the 43 papers in the Report, all but two are in English, preceded by French and German abstracts. The remaining two are in French and German with English, German, and English, French abstracts, respectively. The report is well illustrated and well printed.

⁵ Zimmerman, P. W., Oxygen requirements for root growth of cuttings in water. *Loc. cit.* footnote 1, pp. 170-186.

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WHO'S WHO AMONG THE PRAIRIE GRASSES ¹

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For many years I have lived on the prairie, where I became familiar with the grasses. Each spring I have been delighted with their renewal of growth—in watching the brown landscape of rolling hills become carpeted with green. Year after year, with the progress of the season, I have seen the changing aspects, which, with the coming of autumn, end in the wonderful coloration of the prairie grasses. But the prairie as a whole has seemed a somewhat elusive thing, difficult to visualize, not easy to describe, indefinite and extremely variable in its composition. This vagueness of understanding, I believe, has been shared by other students of prairie. A careful survey of the literature reveals scarcely a single contribution that gives a clear idea of the structure of the vegetation, *i.e.*, what the dominant species are and why they are dominant; what patterns or types of grassland occur in prairie; where they occur; their relative importance; and to what degree the various species intermingle to form them.

TALL-GRASS AREA STUDIED

I finally decided that the real difficulty, in my own case at least, was a lack of definite information. Perhaps I did not *know* the grasses at all but was merely on speaking terms with them. A central area of tall-grasses right in the heart of the prairie was accordingly selected for study. It was large enough to be thoroughly representative, but not so extensive as to defeat the plan of intensive investigation. It included the tall-grass prairies of the western one-third of Iowa and those of Nebraska. On the south it extended into Missouri and Kansas to the Kansas River, and northward into southwestern Minnesota and southern South Dakota. The plan included a study of 100 typical prairie areas well scattered throughout. So far about 80 have been investigated. Supplementing other studies, there are now several hundred quadrats to determine the exact percentage composition.

¹ Address of the retiring President of the Ecological Society of America, presented at the annual dinner at Cleveland, Ohio, January, 1931.

[*Ecology*, Vol. XII, No. 3 (pp. 455–621) was issued July 23, 1931]

REPRESENTATIVE TALL-GRASS AREAS STILL REMAINING

After careful searching, it was gratifying to learn that representative areas of grassland are still to be found. They sometimes occupy the rougher lands but frequently occur on level or slightly rolling ground. Such areas, varying in size from 40 acres to a square mile, have been found here and there throughout, and in many places native grassland is still abundant. Where the land has been kept as Indian reservations, extensive tracts of prairie still remain—as my good friend in Kansas expressed it—just as God left them.

All of the prairie areas are disturbed, usually, only by late annual mowing. To what extent, if any, they have been modified from the original grassland (which was both grazed and burned) can not be determined. But their resistance to invaders, even when the area is entirely surrounded by them, shows in an impressive manner their high degree of stabilization and their wonderful adjustment to the environment.

That the prairies are making their last stand against the invader—man—can not be overemphasized. Detached areas are even now often separated by many miles. Every year some of these scattered relict outposts are yielding before the plow or being destroyed by intensive grazing.

After considerable study, it was found that the complex, intricate, and apparently endlessly variable cover of grassland resolved itself into a few distinct types. Further studies revealed that each type was characterized by only one or a few really important grasses. While there is variation within the type or pattern, and considerable alternating and overlapping, yet once the types are recognized the whole prairie problem is greatly clarified.

LOWLAND TYPES

The big bluestem type is the most representative, most extensive, and most important of those found on the lowlands. It is characterized by the single species, *Andropogon furcatus*. This species is one of the two most important dominants of prairie. Together with little bluestem (*Andropogon scoparius*) of uplands, it constitutes fully 70 per cent of the entire grassland cover. It is more mesic than the little blue stem and is best developed on lower slopes and well aerated lowlands. It is not confined to them, however, but is represented in practically every square meter of the little bluestem type of uplands, where it constitutes, on an average, 25 per cent of the plant cover. It does not thrive in soil that is frequently saturated, and under such conditions it gives way to slough grass (*Spartina michauxiana*). Almost pure stands occur over extensive areas, except for a small admixture of bluegrass (*Poa pratensis*), Indian grass (*Sorghastrum nutans*), and a few non-grassy species. The actual plant cover within this type averages 80 per cent big bluestem; it frequently runs as high as 90 per cent, and rarely falls below 60.

The causes of dominance of big bluestem are found in its rapid growth, dense, sod-forming habit, and great stature, as well as its tolerance of shade. Seedlings develop rapidly. A height of 12 to 18 inches and a root depth of 2 to 4 feet may be reached in a single summer. The tillering habit is pronounced. Seven or 8 weeks after germination, tillers begin to appear, and soon the seedling develops a small tuft or bunch. Rhizomes are also quickly produced, and the area occupied by both shoots and roots is thus greatly increased. Both seedlings and mature plants are very tolerant of shade. The leaves remain green and manufacture carbohydrates under light intensities of only 5 to 10 per cent.

As a result of the rhizome habit, *Andropogon furcatus* typically develops a characteristic sod. The individual stems are usually spaced more than a centimeter apart. Even in the densest clumps they average less than one per square centimeter. Moreover, between the mats of sod there is much unoccupied soil. The total ground cover in this type rarely exceeds 25 per cent. Notwithstanding this open spacing, the foliage is so dense and the light so greatly reduced that invasion is extremely difficult. It is more or less successfully accomplished by bluegrass, and easily so as a result of annual mowing. *Andropogon*, being a genus of southern extraction, renews growth rather late in spring—usually about mid-April, and several weeks after the appearance of *Poa*. The bluegrass may even blossom before it is much shaded by its big competitor. *Poa* was found in the big bluestem type nearly 80 per cent of the time. It formed from 1 to 15 per cent of the total ground cover. But on the upland where the tall stems of *Andropogon furcatus* are often too few to greatly reduce the light, invasion is more readily accomplished. Quite in contrast is the very dense growth of *Andropogon scoparius*; the area actually covered by this species is rarely invaded.

The development of the shoots of the big bluestem in the perennial sod is rapid. By the first of June the average height is normally about 12 inches, and by July, 18 to 24 inches. The flower stalks begin to appear above the general level of the foliage early in July, but anthesis does not reach its maximum until late August or in September. On dry slopes flowering may not occur except during very favorable years. Here flower stalks only 3 feet tall and with a single inflorescence are not uncommon. But in the lowland, both flower stalks and spikes are extremely abundant and well developed. For example, along the Missouri bottomlands the foliage of this rank grass reaches a height of 3 feet and the flower stalks 8 to 10 feet.

What chance has any other grass against such a formidable competitor? The answer is, little or none. Only one other species approaches it as an ecological equivalent, and that is the Indian grass (*Sorghastrum nutans*). It is, however, of far less importance. This species is most abundant in Kansas, where it may very locally constitute 90 per cent of the vegetation but more usually only 5 to 15. Throughout the region as a whole, Indian grass was found in only one-third of the quadrats. The usual percentage

was from 1 to 3, and in many lowlands it was almost absent. It typically occurs in the dense bluestem sod as isolated stems or very small clumps. Its large seeds are remarkably viable, and germination is high. This grass is of approximately the same size as big bluestem, makes the same rapid growth, and is also very tolerant of shade. It thrives in areas occasionally denuded by floods or repeated fires. In fact, its abundance usually indicates disturbance. The weak spot in its life history is its inability to tiller and form rhizomes under competition, and thus to extend its territory. Big bluestem is more prompt and more vigorous in this strategy, and consequently it possesses the land.

A second type of grassland pattern is that dominated by slough grass (*Spartina michauxiana*). This species is really not a dominant of low prairie but is the final consociates of the hydrosere leading to the prairie proper. It grows typically at the edge of sluggish streams or ponds and in water-logged or wet soil, rarely occurring in moist soils except in dry seasons or as relicts in soils that have been drained.

Its demarcation of soils too wet and consequently too poorly aerated for the growth of maize is clearly shown throughout the prairie. In countless areas the uplands and big-bluestem lowlands have been broken, but the slough-grass draws and flooded lands have been left intact. They are too wet for cropping, at least in spring, but furnish excellent hay, and very successfully hold the soil against erosion. Vast areas of "first bottom" along the Missouri and its tributaries are covered with *Spartina*, often in almost pure stands. Towards the mesic side it gives way to big bluestem, usually through a transitional type to be described.

Spartina plays the rôle of a dominant because of its tall growth in dense, pure stands. Light values near the soil surface are often only 1 to 2 per cent and the shade is equalled only in the densest climax forests. Seedlings grow vigorously in wet, bare areas and to a height of 3 to 4 feet in a single summer. But reproduction, except in such areas, is undoubtedly almost entirely by means of the extensive underground stems. Beneath mature plants the soil is filled with a mat of coarse, woody, very much branched rhizomes. These extend outward 2 to 15 inches before giving rise to erect shoots. The depth of root penetration is surprising, considering the water relations of the habitat. Depths of 8 to 10 feet are commonly found in wet soil. This grass has coarser roots than any of those of the prairie proper.

Although slough grass renews activity rather late, often not until the second week in April, it grows more rapidly than any of the prairie grasses. By the first of June it is frequently in the sixth leaf stage and varies from 2 to over 3 feet in height. Where it shares marginal areas with other grasses it conspicuously overtops them. The general height of leaves at the end of the growing season is 3 to 7 feet, depending upon the water supply. Because of the extensive rhizomes, it always forms a sod. Where best developed, the coarse, woody stems are widely spaced, and the soil surface

actually occupied is often only 1 to 3 per cent. In the dense shade 2 or 3 of the basal leaves are usually dead by midsummer, leaving the stems bare to a height of about 8 to 12 inches. Even in moist soil the flower stalks are 5 to 6 feet tall and in wet areas they often reach 9 to 10. Where an abundant and constant water supply favors the growth of *Spartina*, other prairie grasses are effectually excluded.

An intermediate lowland type of much less extent than either of the preceding occurs between the big bluestem and the slough grass areas. It is characterized by two species, tall panic grass (*Panicum virgatum*) and nodding wild rye (*Elymus canadensis*).

Panicum virgatum is a tall, coarse, sod-forming grass and an important dominant in low, moist soil. It is perhaps the most mesic of prairie grasses as is shown by its abundance in the drier portions of the *Spartina* consociates, occupying with wild rye and red top (*Agrostis alba*) areas that are too poorly aerated for the growth of big bluestem. It is rarely found in extensive pure stands, the clumps and areas usually alternating with slough grass, sedge (*Carex vulpinoidea*), etc. In such mixtures it covers many square miles of poorly drained bottomlands along the Missouri and its tributaries, constituting 10 to 30 or more per cent of the vegetation. With wild rye it is almost invariably found as a transition species along ravines and draws wherever big bluestem gives way to slough grass. The transition, whether gradual or abrupt, is characterized by small areas of *Panicum* in dense, pure stands, by clumps often 3 to 4 feet in diameter, and by an intermingling with the bluestem on its marginal areas. While it may locally constitute 25 per cent of the grass mixture, it often falls to 10 per cent, and where *Andropogon* is well developed, to less than 3. It is also found in areas of higher water-content at the heads of broad, sloping flats receiving run-off water. The rank growth at the bottom of ravines where it is often 6 feet high, gradually decreases to about 3 feet near the top. Moreover, the dense sod becomes thinner as the grass extends its area into drier lands until only scattered, dwarfed, individual stems occur.

Panicum is of tropical derivation and consequently more important in the south and east portions of the area where the climate is more humid as well as warmer. It is largely replaced northward by *Elymus*. Seeds of *Panicum* usually give a low rate of germination, and propagation is undoubtedly largely by rhizomes. The seedlings develop rapidly but are less tolerant of shade than are those of the big bluestem. It renews growth late in spring but owing to an abundance of food in roots and rhizomes it develops rapidly and is often 18 inches tall by the first of May. Because of the lack of basal shoots and the wide spacing between stems, only a small amount of the surface soil is actually occupied. But the foliage is luxuriant, and only the most tolerant of lowland species such as big bluestem can grow in the shade of this dominant.

Elymus canadensis is also a tall, coarse grass of about the same stature as *Panicum virgatum*, and, like it, has a high water requirement. Although of

wide and regular distribution, it is of minor importance over the prairie as a whole. It is typically a lowland species, reaching its best development in the wet transitional areas between slough grass and big bluestem. It also intermingles more or less with both of these. It forms pure stands only in very small areas. Usually it constitutes a 1 to 5 per cent mixture among the other grasses, and exceptionally 10 to 15. Among 300 quadrats in low prairie, this species occurred in only 32, and it never exceeded 2 per cent in abundance. On uplands, wild rye is found only where local disturbance has occurred, as about gopher mounds, badger holes, etc. It forms a reliable indicator of increased water-content due to local denudation on upper slopes and ridges. Once in possession, the bunches or clumps may remain many years.

Northward and westward, *Elymus* becomes more abundant than in the south and east. Here, on level land subject to overflow and too wet for big bluestem, it often covers large tracts and resembles thinly planted fields of barley. Examination shows that the abundance is more apparent than real. Rarely more than 40 to 50 stalks occur per square meter. Since there are few or no basal shoots or leaves it may form only 5 to 8 per cent of the ground cover.

The relatively large seeds of *Elymus* show a high rate of germination. Unlike most grasses, they germinate well even when covered with soil to a depth of 2 inches. Early in August, a height of 6 to 10 inches is attained, and sometimes flower stalks are produced the first season. Tillering begins early, the short rhizomes resulting in the formation of bunches or clumps. Because of its northern extraction, growth is resumed very early in spring, 2 or 3 weeks before that of its competitors. This is distinctly advantageous to this species in its competition for light.

UPLAND TYPES

The most important and most extensive of upland types is that characterized by little bluestem (*Andropogon scoparius*). Just as big bluestem is the most important dominant of low prairie, so also little bluestem forms the great bulk of the upland grass cover. It easily exceeds in importance all other upland species combined. In the south and east, where moisture is more plentiful, its chief competitor is big bluestem. In the north and west, especially on poor soils and areas with extreme run-off, little bluestem intermingles with needle grass (*Stipa spartea*) and in places is almost replaced by it.

Little bluestem ordinarily forms an interrupted sod, which is best developed northward. The mats or tufts are so dense that few other species can invade them. Accompanying species grow between the mats. Where the slopes are steep and run-off and erosion great, the bunch habit becomes pronounced.

On the deep soils of steep loess hills, little bluestem alone frequently constitutes 90 per cent of the vegetational cover; and, over the area as a whole, including level uplands, 50 to 75 per cent. On midslopes and lower hillsides it intermingles with the big bluestem, often on equal terms. On lower lands, the big bluestem and other tall grasses have the decided advantage in securing light, and, if there is sufficient water for a continuous cover of the taller grasses, little bluestem entirely disappears.

The percentage of germination of little bluestem is often low, but the seedlings are vigorous. During the first summer they reach a height of 6 to 8 inches, and tiller profusely. The young roots are fine and extremely well branched. Thus the plant is well fitted to absorb in relatively dry soil. In the absence of competition it may complete its life cycle by producing flower stalks and seeds the first year. But in the prairie, this requires 2 seasons very favorable for growth, and ordinarily 3 or more.

The mature root system consists of a vast network of threadlike roots and masses of finely branched rootlets. Thus the soil beneath the sod mat, and for several inches on all sides of it, is filled with roots to a depth of about 5 feet. Such an absorbing system is wonderfully efficient.

The leafy stems grow compactly in the sod mat. There are often 200 to 300 in a single square decimeter. Many of these are furnished with several tillers each, and all are leafy to the base. Thus there is little room for invasion. The density of the mat varies with the water relation and also with age. On lower slopes the whole sod may consist of closely crowded stems, but on uplands, and especially during dry years, the center may have few stems and the peripheral ones show a much better growth. Deterioration of the clump nearly always occurs first in the older, central part and proceeds toward the periphery.

The size of the sod mats is variable. In favorable situations solid clumps 1.5 by 2 feet in extent may be found. But normally they are smaller, often 6 to 8 inches or less, and the shape is irregular. Often the sod consists of smaller tufts rather closely aggregated so that the overlapping leaves give an apparent cover of 80 to 100 per cent. Actually the basal cover in any case seldom exceeds 25 per cent. Larger and better filled clumps occur southward, while the best development of the tufted, sod-mat type is found in northern Nebraska and Dakota. The height attained by this species is variable. It ranges from 7 inches on dry hilltops and regions of lowest rainfall to 22 in the warmer, more humid southeast. On moderately low lands, in competition with the taller grasses, heights of 3 feet or more are attained.

Flower stalks begin to appear by the middle of August. These vary in height from 1.5 to 2 feet on dry uplands, where blossoming may occur only during exceptionally wet years, to 3 to 4 feet under a more favorable water supply. Flower stalks are usually thickly grouped, and seeds are produced in great abundance. By early winter nearly all have been dislodged

by the wind, but the old flower stalks persist a long time. The wonderful coloration of the prairie in late autumn is due largely to the drying bluestems.

Of the two other upland patterns, that formed by the needle grass (*Stipa spartea*) is the most important. This bunch grass is typically an upland species. It is practically of no importance in the Kansas and Missouri portions of the area, but it gradually increases in abundance northward and becomes an important prairie component. Steep, dry ridges and xeric slopes, especially where the soil is thin and perhaps sandy or gravelly, are frequently more or less dominated by *Stipa*. Such areas alternate with the little blue-stem pattern or with that of the drop seed (*Sporobolus heterolepis*). Its chief associates are June grass (*Koeleria cristata*) and little bluestem but it is found in various grassy mixtures.

Because of the excellent growth of *Stipa* on dry banks along roadsides, and its very deceptive appearance as regards abundance, its frequency and importance are easily overstated. Even where the bunches are a foot apart, the widely spreading leaves and gracefully bending stems, which may extend 1 to 3 feet on all sides of the clump, give the appearance of a thick growth. A study of the composition of the vegetation in which *Stipa* appears to dominate shows that it really constitutes only 15 to 35 per cent. Rarely it makes up 50 to 80 per cent of the plant cover, and this only in small areas. In many prairies it is scarcely represented, and usually it forms 1 to 3 per cent of the vegetation as a whole; but in hilly lands, in the central and northern part of the area, alternates with an abundance of *Stipa* may cover from one-fifth to one-third of extensive uplands. Moreover, it is frequently more or less abundant on flat lands at the heads of draws, and is readily distributed over broad washes on lower slopes that are subject to overflow and deposit during exceptionally heavy rains. Here it is found with big bluestem usually in no great abundance but sometimes dominating local areas.

The large, heavy, long-awned seeds of *Stipa* germinate normally only after being worked 1 to 3 inches into the soil. The seedlings make a good growth, and by midsummer the parent culms are often a foot tall and well furnished with tillers. By this time the fine, well branched root system is usually 1.5 feet deep and in good contact with the moist subsoil. True to their boreal extraction, year-old *Stipa* seedlings begin growth in March. They are 3 to 4 inches tall and in the third- or fourth-leaf stage before most other grasses have broken their dormancy. By the second summer the foliage may reach a height of 2 to 3 feet, but the production of flower stalks ordinarily does not occur until the third year. The root system of even mature plants seldom reaches depths beyond 2.5 to 3 feet, but it is exceedingly well fitted for absorption from the upper levels.

The production of tillers and short rhizomes gives rise to more or less circular clumps or bunches; needle grass never forms a sod. The size of the clumps is variable, depending upon conditions for growth; some are only one-fourth inch in diameter, the largest perhaps 5 inches. Wherever *Stipa*

is at all abundant, the ground cover is very open, and the greater the apparent density of the species the more bare soil. Often only 5 to 7 per cent of the soil surface is occupied. Small tufts may have only a single flower stalk, but large clumps often produce 18 or more. By June 10, the twisting awns indicate the ripening of the seeds, and by the first week in July the seeds have fallen and are widely scattered by the wind. The excellent method of planting the seed compensates the small numbers, usually only a dozen or two per flower stalk.

The bases of the long, spreading clusters of rosette-like leaves often remain green all winter, and growth is resumed with the first warm days. As a result of its early growth it avoids excessive competition.

Stipa, accompanied by *Koeleria*, represents an earlier stage in development than do the andropogons.

Koeleria cristata is also a bunch grass, but of smaller stature than any of the preceding. Like *Stipa*, it is of boreal origin and is more abundant in the northern part of the area. It shows a decided preference for dry uplands, and is typically associated with needle grass, drop seed, and little blue-stem. Not infrequently, however, it occurs also on lower mid-slopes, and, in lesser abundance, on well-drained lowlands.

In many prairies, especially southward, this species may be scarcely if at all represented, but it more usually forms 1 to 3 per cent of the cover, at least locally. An abundance greater than 5 to 10 per cent is rarely found except in disturbed places.

A minor and final upland prairie pattern is exhibited by *Sporobolus heterolepis*. This species of drop seed is distinctly a bunch former. Notwithstanding its wide distribution, it is not found in many of the prairies. It is always most abundant on the driest uplands where it may dominate local areas, forming 80 or more per cent of the vegetational cover. More usually it occurs as scattered bunches intermingling with needle grass and little blue-stem where it may constitute anywhere from 1 to 20 per cent of the cover.

The bunches are usually about 5 inches in diameter, but larger ones up to 18 inches occur. They deteriorate as a result of the death of the central part, and often break up into numerous tufts which give the appearance of a loose, open, discontinuous sod. The stems are so densely aggregated that no other species can invade the tufts. The plant early renews growth, and the foliage reaches a height of 10 to 18 inches. The long, attenuated leaves do not stand erect but curve gracefully, so that the top of the bunch much exceeds the basal area. For example, in a typical area where this species constituted all but 2 per cent of the vegetation, the apparent cover was about 99 per cent, yet less than 10 per cent of the soil surface was occupied. Underground, however, the whole soil mass was preempted by roots. Once in possession, it keeps its holdings against all invaders for long periods of time.

SUMMARY

We may summarize by saying that the bluestems are the aristocrats of the prairie. Their holdings are by far the most extensive. *Andropogon furcatus* has almost complete possession of the best lowland soils, sharing them only in a very small way with *Sorghastrum nutans*. It keeps out invaders, except a limited amount of *Poa pratensis*, by its dense shade.

Andropogon scoparius possesses the uplands. It holds them against invasion by its dense aggregation into sod mats, and appropriates most of the water-supply by virtue of its wonderfully efficient root system.

On the lowlands, only the less desirable, poorly aerated soils are held by *Spartina michauxiana* and the transition to well aerated ones by *Panicum virgatum* and *Elymus canadensis*. On the uplands the thinner, poorer soils, as a rule, are possessed by *Stipa spartea* or *Sporobolus heterolepis*, and even here *Andropogon scoparius* contests for possession. *Koeleria cristata* associates with all of these land-owners but rarely has holdings of its own.

Hence, in a "Who's Who among the Prairie Grasses" *Andropogon furcatus* and *Andropogon scoparius* would be found in bold type and their accomplishments would cover several pages. Ordinary type and a single page would be sufficient for *Spartina* and *Stipa*, while *Panicum*, *Elymus*, and *Sporobolus* would probably each receive but a single paragraph. The names of *Poa*, *Sorghastrum*, and *Koeleria* would correspondingly be in 6 point. Few other grasses have sufficient importance to be included.

QUANTITATIVE METHODS IN THE STUDY OF NUMBERS OF TERRESTRIAL ANIMALS IN BIOTIC COMMUNITIES: A REVIEW, WITH SUGGESTIONS¹

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General Remarks

In the investigation of the basic interrelations of terrestrial plants and animals in natural communities, it is essential that information as to the exact or the approximate numbers of animals present should be obtained. Not only is information required as to the number present at any one time, but also as to the variation in numbers in selected communities according to seasonal and other conditions. Upon knowledge of the absolute numbers and of the variations in numbers of animals from period to period, it is possible to base conclusions as to the influences of given species of animals in given biotic communities. It is to be noted that not only is this knowledge likely to throw much light upon the structure and development of natural communities, but also has definite practical uses in the fields of economic entomology, range, forest and agricultural practice, and the investigation of such diseases as plague, human and animal trypanosomiasis, and malaria.

From the general standpoint, Elton ('27, '29) has drawn attention to the importance of studying the numbers and the variations in numbers of various animals, while the work of the U. S. Biological Survey upon the relations of rodents to range management should make the most sceptical realize the earnest necessity of knowing more about the matter of animal numbers. In such problems as that presented by the tsetse-fly in Africa, there is an ever-increasing demand for data regarding the numbers of animals of different species in different communities at different time and under definite conditions.

As Elton ('27, p. 101) has pointed out, we know very little about the matter of animal numbers. The field is a new one, and as yet the methods employed are empirical and not satisfactory—there is much scope for broadly trained field workers gifted with imagination of the right type, to evolve new and improved ways of obtaining quantitative data. Methods employed by ecologists studying vegetation quantitatively are applicable directly in a few instances only—special methods are needed.

I have referred to the *biotic community*—a brief explanation of this term

¹ Abstract in South African Journal of Science, 1930.

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is necessary. As regards the relation of plants and animals in natural conditions, there are at present three general concepts. Firstly, most plant ecologists consider that the plants really form the community and that animals are to be held as *external* factors, even as the physical factors. Secondly, some animal ecologists state that from the view point of the animal, the plants form part of the habitat, and should be considered apart from the animal community. Finally, there is the concept supported by Clements and his collaborators, Shelford and his associates, and myself, that plants and animals are interrelated, coacting members of an integrated *biotic community*. This concept, which I have dealt with at some length elsewhere (Phillips, '31), has the virtue of focusing attention upon the reciprocal relations of plants and animals, and avoids doing violence to the facts of nature. I refer to it here with the desire of emphasizing that in the study of animal numbers, the data obtainable are only of value to the degree in which they are accompanied by evidence regarding the plants and the other species of animals associated with the particular animal under study. To anticipate criticism from those who hold that work reminiscent of the proverbial counting the pebbles of the shore is so much wasted effort, I stress the absolute necessity of gaining in addition to the numerical data, observational and experimental data as to the habits of the animals, the interrelations of animals and plants, and the physical habitat. In this paper I confine my attention to a consideration of the methods of studying animal numbers.

Objects

As the literature on the methods of taking quantitative samples of animals, is somewhat scattered, my first aim is to bring together such references as are relevant. It will be seen that the information in the literature is neither full nor yet remarkably satisfactory. My second aim, therefore, is to make such suggestions, where possible, as may seem useful. Finally, I hope to interest younger workers in biology in this field which is not only fascinating but important.

Methods of Determining Numbers in Certain Types of Animal: References and Suggestions

For the sake of brevity and convenience, the subject is considered under appropriate animal-type subheads, while the principal literature and my own suggestions are considered in natural relation one to the other.

That two inherently different types of enumeration are involved is clear. In one type there are the methods having as their sole object the enumeration of animals once and for all: the site may be disturbed, the animals may be either put out of equilibrium with their natural setting, or may be killed. The second type has regard to methods making possible the periodic resampling either of the same site in the same community, or at any rate of a site in close proximity to the earlier site: the natural setting must be maintained as much

as possible, and the animals must be disturbed to the minimum. Obviously this is an infinitely more difficult object to attain than that of the first type.

I. SOIL AND SUBSOIL INVERTEBRATES

In usual practice the most important forms are the Protozoa and Arthropods.

Points of practical importance in sampling soil organisms are: (i) Use the plant covering as an index, that is, take the samples in accordance with vegetation types. (ii) Select positions that are representative of the soil generally, that is, do not take as representative samples, portions from either very wet or very dry, very deep or very shallow very bright or very dark sites—unless these samples be labelled as coming from such exceptional sites. (iii) Undisturbed sites are more suitable than disturbed ones, provided the subject of disturbance effects is not under special study. (iv) In all instances give information as to the nature, and if possible, successional stage of the vegetation, references to prevalent or exceptional physical conditions, aerial and edaphic, and notes upon the general history of the community, especially with respect to the action of man. (v) As large a number as possible of samples should be taken: when areas are under intensive study by quadrat methods, at least 5 per cent of the area of such quadrats should be sampled.

As the investigation of soil protozoa is a highly specialized task, investigators who are not especially trained in protozoology, should take the samples, preferably per unit volume or unit weight—for example, 1,000 c.c. or several kilogrammes of soil—place them in aerated metal receptacles, and submit them to a protozoologist. It is advisable to take the total moisture content of the soil, the maximum water-retaining capacity, the permeability, the pore-volume, the rate-of-air-flow, and the hydrogen ion concentration, from the soil immediately to the side of the sample.

In the absence of a trained protozoologist, the total number of protozoa active and encysted may be obtained by following the method described by Cutler ('20), Cutler and Sandon ('22), and by Emerson ('25); but it is doubtful whether this information is of any value in the absence of identification of the principal forms.

A very fair amount of work has been done upon the insect fauna of soils, especially by McAtee ('07) who investigated to the depth that a bird could scratch, Cameron ('13, '16), Beebe ('16), Wolcott ('18), Buckle ('21, '23), and Morris ('22).

Perhaps the most systematic methods as yet published have been those of Shelford and his associates. Sanders and Shelford ('29, p. 308) employed an inverted can, of internal diameter 25 cm. (10 inches), pressed firmly into the soil; through an aperture they applied a mixture of chloroform and petrol to the surface of the soil, thus killing the fauna. The soil ultimately was sieved, and the various organisms classified and enumerated. They endeavored to correlate the number of organisms thus caught with the number cap-

tured in the herb, shrub and tree strata of the same community, and considered that *three* sweeps of the net yielded essentially the same number of animals of the same forms from the vegetation as *one* bucket capture from the soil surface. Weese ('24, p. 10) varied the method somewhat. He placed the leaf litter and other debris upon an area of 2 feet square within gauze boxes, and etherized the animals. He then dug the same area to a depth of 10 cms., placing all the organisms obtained in vials. His methods were applied several years later by Blake ('26, p. 55). The method was again varied by V. G. Smith ('28, p. 485) who examined the organisms in the leaf litter collected from 1 square foot, and from the soil to a depth of 10 cms. She then reduced to the same unit—one square meter—the organisms caught in the aerial layers above the soil, by multiplying the number of organisms in the litter or in the soil stratum by 12. This factor was derived from the results of several comparisons between the number of animals taken in 50 net sweeps in the herbs and the average number of the *same forms* killed under an inverted can enclosing a measured surface. Another Illinois student, Shackleford ('29, p. 126), later used the same methods in the prairie, the size of the area being 0.5 square foot only, and the factor by which the number of soil insects was multiplied to bring them to the same unit as the insects of the same species in the aerial layers being 20.

Werner Herold ('28, '29) has recently employed the 30-minutes' search basis for a quantitative study of surface Isopods and Diplopods, but apparently used no unit of area.

To accelerate the separation of soil organisms from the soil matrix, Morris ('22*b*) has used a simple soil washing apparatus. Shelford ('29, p. 44) suggests the use of a very large Berlese (water-jacketed) funnel. Debris is placed in a container with a coarse screen bottom immediately above the mouth of the funnel; as the animals are warmed by the heating of the water in the funnel, they fall through the screen into a receptacle.

Methods used successfully by myself are as follows: (i) A mild steel cylinder of 1,000 c.c. capacity³ is hammered into the soil until the rim is flush with the surface; a metal lid is placed over the rim. A spade is dug into the surrounding soil so that the whole cylinder is lifted with its contents, a second lid being placed against the lower rim. The 1,000 c.c. of soil is then searched either by direct inspection or by means of a washing apparatus. This is a rapid method, and enables a fairly large number of uniform-size samples to be taken from any community. For surface forms the cylinder is somewhat too small. (ii) For surface forms and also for larger subterranean organisms, such as earthworms and larger Coleoptera, I have employed analysis circles of one square meter; these are described by means of a radius rod of 56.5 cms. For more widely distributed forms, a 10 square meter circle is preferable—this being described by means of a radius rod of 178 cms. The litter is placed in gauze cases, is carefully searched, and, with

³ Specially made by Messrs. Heynes Mathew, Cape Town, at £2/10/0 each.

the animals, is ultimately returned to the site. When subterranean forms are being sought, the area of the circle is dug to a depth of 30.5 cms. (12 inches), searched *in situ* for larger forms, and then the soil is brought to the laboratory to analyze for smaller forms by washing. If the washing be done in water, most of the organisms escape uninjured; specimens are kept for identification, then the soil and the remaining organisms are returned to the original site. It is realized that this disturbance of the organisms and the production of entirely different conditions of aeration and water-content in the soil rule against the later use of the same portion of ground. My practice is to select an undisturbed portion of soil the nearest edge of which is not less than the diameter of one analysis circle from the original site. In practice the vegetation of the circle is recorded according to species, height, and nature of shade cast. (iii) In the investigation of the distribution according to particular features of soil or shelter, of puparial forms (*e.g.*, the puparia of tsetse-fly), and in the study of distribution and numbers of widely dispersed adult forms, belt transects have been found very useful. These may range from a few centimeters in width to a dozen feet, and usually are not less than several hundred yards in length. The organisms under investigation are collected from this belt, decimeter by decimeter, their distribution, if necessary, being charted upon suitably printed belt-transect charts. Such transects are especially useful when it is desired to contrast the fauna of two contiguous vegetation types, the faunistic differences over the type, and the transition zone or ecotone, being shown graphically. Features in the soil texture, moisture, litter, vegetation, light intensity and the like, may be recorded *pari passu* with the numbers of organisms, unit area by unit area. I have found this method very useful in the study of correlation of earthworm numbers with forest-type, while my colleague Mr. W. H. Potts is applying it to the statistical study of distribution of puparia of *Glossina morsitans*, one of the tsetse flies. (iv) Shelter and breeding sites may be prepared from natural materials, so many per selected area. These should be examined at definite intervals. To provide against fallacious results, the removal from the area and surroundings of shelter or breeding sites other than those experimentally provided, must be arranged. This method has no wide application, and is of use upon relatively small sites only. Its value in the instance of tsetse fly has not been great, owing to the very large number of natural sites readily available.

2. AERIAL INSECTS: PHYTOPHILOUS

For clarity I will discuss the methods of capturing aerial forms other than those definitely attracted to man or animals, under the subheads: (i) netting, (ii) light traps, (iii) bait traps, (iv) mechanical traps, (v) "liming," or the use of adhesives.

(i) Netting

So far as I am aware, the only quantitative netting methods attempted have been those of Shelford and his students. Sanders and Shelford ('29,

p. 308) examined the fauna of herb, shrub and tree layers of a Pine-dune community, making 4 strokes in each level, by means of a net of 30 cms. diameter, and handle length 70 cms. They endeavored to reduce the collections made with the can mentioned under (1) Soil Invertebrates, to the same value. Weese ('24, p. 10), examining herb and shrub layers of a wood, took samples based upon 10 short sweeps through the vegetation with a net of 30 cms. diameter. He states that, assuming the average depth of the foliage of either the herb or the shrub stratum to be 0.5 meter, and the average length of the sweep of the net to be 1.0 meter, 10 such sweeps include approximately the volume of vegetation above the unit area.

Blake ('26, p. 55) employed essentially the same method in studying the several strata of a coniferous forest. Fifty sweeps per stratum were taken by V. G. Smith ('28, p. 485) as representing the amount of life per square meter in the shrub and herb strata of a deciduous forest succession. The collections from the leaf-mat and ground were multiplied by 12 to bring them into the same unit; the factor adopted, 12, being the result of several comparisons between the number of animals taken in 50 sweeps in the herbs, and the mean number of the same forms killed under an inverted can enclosing a measured surface, with its vegetation. This factor was used as representing the mean efficiency of the netting, disregarding the time of day and the type of weather. Shackleford ('29, p. 126) applied identical catching and comparison methods, but found that the factor 20 was required to bring the number of organisms of the leaf-mat to the same unit—the square meter. According to Shelford ('29, p. 45), King has used a stroke 1.5 meters in length with a 35 cm. folding net, at such intervals as would make each stroke the first disturbance of the vegetation covered, the strokes being made progressively in one direction, and with the same distance between the strokes throughout.

In considering the sweep-net method, I am convinced that it is impossible to apply an unswerving routine of sweeping—the reasons being that the numbers, liveliness and rate of flight, vary so greatly according to vegetation and to such physical factors as light, temperature, rate of evaporation and force of wind. To my mind, it is infinitely more satisfactory to ignore the number of sweeps made, but to pay precise attention to the catching of all the organisms actually seen *within a unit area within a definite period of time*. Owing to the probable disturbing and driving away of the insects as the result of sweeping, it is clearly advisable to catch along a narrow transect or upon a small circular zone up to several meters in diameter, rather than upon a relatively extensive rectangular, square or circular area. Either the insects should be removed from the net at short intervals and placed temporarily in vials, or a “one-way” net, with a flap allowing of capture but not of escape, should be used.

Very little is known regarding the influences of the catching party upon insects that are non-blood-feeding. In the event of there being either a defi-

nite deterrent or preference influence, it would be essential to maintain the catching party at a definite number, so as to provide the same influence, catching period by catching period.

It is to be noted, too, that, as insects exhibit variation in flight of the sexes, move from stratum to stratum, and even from vegetation type to vegetation type, from hour to hour, from day to day, and from season to season, and, as they undoubtedly are influenced as to behavior by development of the plant succession, it is necessary to make sweep-catches during morning, noon, afternoon, and evening hours, and upon several days at least, per week, throughout the seasons. Scattered random sweepings are of no quantitative value, and may be highly misleading if employed in drawing conclusions. In all other quantitative methods, there must be no undue haste to interpret data collected from short-period observation.

(ii) Light Traps

Owing to certain insects, and in some instances the male element of species (see Bensel, '16, Turner, '20, Williams, '26), being attracted to lamps, a number of investigators have used light traps. Unfortunately almost all the work done has been non-quantitative.

It is important that the light should be kept at a definite intensity, that it should shine from all sides as well as from the top, and that there should be provision for the protection of the insects from charring and burning. Koch ('24) and Williams ('26) have described useful types of traps.

There is no doubt that light traps are less selective than bait traps, a larger number of types and species being attracted (see Cook, '20, '26, '27). Organisms that are naturally negatively phototropic are repelled, and, for some unknown reason, many positively phototropic forms are not attracted. A combination of bait and light at times produces better results than the light alone, but the difficulty is to maintain the standard of the attractiveness of the bait—which changes according to period of exposure and nature of the weather.

To test the utility of the light trap in the study of a biotic community, it should be determined what groups or species are not being attracted. Those forms attracted should have displayed for their attraction a standard light, within a definite plant community, large enough to prevent the light being noticeable from contiguous communities, for a standard time. Useful aids to capture are mechanical traps and sheets of adhesive substance near the lamps; in addition the lamp is usually placed upon a stand within a wide moat of water, into which the insects fall. Another effective method is to place rapidly over the lamp and the associated organisms, a light gauze casing of about 27 cubic meters. Specimens may be retained for study, and the residue rejected, the lamp being extinguished before the site is left. The traps should be displayed during various hours of the night, and over the seasons.

(iii) Bait Traps

In the study of phytophilous insects, traps of food, odoriferous substances, or material for breeding, are of limited use in quantitative work. They are highly selective as to forms attracted, and are distinctly liable to vary according to age of the bait and to weather conditions. Unless poisons are associated with them, they are not susceptible of accurate searching; if poisons be applied, the animals are either killed or physiologically disturbed.

In my own experience (Phillips, '26), baits are of use in the study of pollenating insects. Honey and other bees and Lepidoptera may be attracted by either baits of honey and sugar, or by definite-sized bouquets of flowers displayed for a definite time, or by a combination of these attractants. The number of visiting bees is recorded by direct observation. Some excellent quantitative work in this connection has been accomplished by Clements and Long ('23).

(iv) Mechanical Traps

Mechanical traps are usually based upon the lobster-pot principle, and must be used in combination with either light or food bait, but have no great value in quantitative work. Probably the only pattern likely to warrant careful trial is that briefly described by Shelford ('29, pp. 44-45).⁴ This is made up of a ring 5 cm. wide and 57 cm. in diameter, which is placed on the ground or held against a tree trunk, and a tight cloth cylinder of the same size, 60 cms. in height, carrying a ring at the top with a 4-bowed hemispherical top closing at the center. The trap is set with the cylinder collapsed and the top open; the cloth parts rest on the soil, 2 vertical guide rods projecting upwards. After the trap has lain in position sufficiently long to allow the animals to assume their natural movement, a spring (*e.g.*, a patent blind roller) is released from a distance; the cloth cylinder is drawn upward, the impact against the tip of the guide rods releasing a second spring which closes the top. In this manner animals above the soil are trapped. The trap requires modification for effective use among herbs and shrubs.

(v) Lining or Use of Adhesive Substances

Although this method has been widely used (see Burgess, '17, Burgess and Griffin, '17, Glenn, '15) capture of insects by means of adhesives is not recommended, in that the materials have to be replaced very frequently owing to the action of the atmosphere, and because the insects themselves usually are injured or killed by coming into intimate contact with the adhesive.

I have found this method of some use, however, in the study of trunk-crawling insects in forests. A fairly successful method is to prepare a smooth surface about 8 inches in width, along the circumference of the tree, and to place upon this, by means of wooden spatulas, a *ridged* band of ad-

⁴ It is possible that the Harris ('30) tsetse fly trap may be useful, as I have seen this pattern capture aerial phytophilous insects.

nesive. Perhaps the most satisfactory are: (a) bird-lime made up as described under "Birds" in this paper; (b) a mixture of Stockholm tar and unboiled linseed oil; (c) Stockholm tar and 10–20 per cent of (volume of the tar) resin; (d) Stockholm tar and 8–12 per cent acetic acid; (e) the commercial adhesive known as "Ratsticker."

Modifications of this method are to place adhesive upon either selected plants or upon selected leaves of certain plants, in herb and shrub strata, or upon certain blades or tussocks of grass. Gauze squares with adhesive thereon may be placed in natural setting among the plants, but are not as satisfactory as the adhesive upon the plant surfaces, as they tend to deter certain insects from settling. An unavoidable feature of adhesives is that they all emit odors, either deterrent or attractive to many insects, and thus exert an unnatural influence.

3. AERIAL INSECTS: BLOOD-FEEDING

Literature upon quantitative capturing of haemophilous insects is practically non-existent, the outstanding exception being work done upon the several species of *Glossina*, or tsetse-flies. On this account, the methods of catching tsetse-fly serve as examples of how to deal quantitatively with blood-feeding insects:

(i) Stand Catching Method

Perhaps the first to apply an approach to a quantitative method of netting tsetse was Carpenter ('12, p. 89), in his work upon *G. palpalis*. He adopted the standing-catch method, whereby a trained native captured all the fly attracted to a single unit area, within a specified time. The total number was reduced to the number per boy per hour. By 1920, Fiske ('20, p. 359), in his investigation of *G. palpalis*, had slightly modified the method of posting trained boys, who stood under large dark umbrellas, at intervals along the lake-shore: Fiske employed a standard net of ring-diameter 8 inches and handle length 18 inches. The umbrellas were considered to attract the fly. Fly were captured and removed from the site. In 1927 the Nigerian investigators ('27, p. 430) recorded that in the capture of *G. tachinoides*, standing catches were made, but in the instance of *G. morsitans* the boys moved about so as to attract the fly. In working with *G. pallidipes*, it is necessary to use bait animals to attract the fly.

Recently the making of quantitative catches of *G. morsitans* has received very careful attention from the Department of Tsetse Research, Tanganyika ('29a, '29b, and Phillips, '30). My colleague, Mr. Potts ('30), has described in some detail the principles governing the making of satisfactory catches. I confine myself to summarizing the more important points.

Tsetse, depending upon such features as physical factors of the environment, animal associates, vegetation type, season, hour, physiological and sexual phases, sex, hunger, number of catchers, the rate of progress of the

catchers and the color of their clothing, may at times be attracted to man, at others may avoid him wholly or partially. The activity of *G. morsitans* as regards man largely depends upon the factors above mentioned, and therefore is a complex response shadowing the density data throughout. For this reason the modified term *density-activity*⁵ is preferable to that of *density* when the number of fly caught under any known set of conditions is being considered.

A point of the greatest importance with tsetse, and a point worth investigating in other blood-taking insects, is that the behavior of the female fly is markedly different from that of the male. Usually, unless well-gorged, the males come to man, whereas the females, unless hungry, either appear in very small numbers or else fail to show themselves at all. This is markedly the case in *Berlinia-Brachystegia* woodland, where female fly are known to be (on account of the large numbers of puparia frequently found therein), but where they show themselves in exceedingly low numbers compared with the males. Apparently the same behavior is shown by certain other Diptera—for example, certain *Culicines* and *Anophelines*.

There are two important methods of catching *G. morsitans*, methods which are applicable to entirely different conditions.

(a) When a systematic fly reconnaissance of a region is required, the fly-transect or fly-round method well developed by my colleagues, Messrs. Nash, Jackson and Potts, is suitable. This consists in the setting out of a lengthy transect traversing not only the various vegetation types of the region, but also game stamping grounds and drinking sites. A body of catchers of unvarying number, in uniform clothing, traverse the sub-transects within each vegetation type according to a definite routine—that is they proceed for 20 to 30 yards, then stop, capture all the fly that appears, on the party or on the ground, then proceed with a second 30 yards, and so on. The movement of the catchers acts as an attraction to the fly. It seems likely that the fly captured is made up of fly of the transect area, and fly attracted from a short distance away.

During the physico-biotic investigation of *G. morsitans* in its natural environment, it is necessary to capture fly upon one and the same general site day by day, or hour by hour. Such sites are within several hundred yards of fixed stations upon which aerial and edaphic factors and vegetation conditions are under measurement. Owing to these stations being visited once or several times daily, trampling is likely to take place, while, in addition, the stations are liable to become impregnated with the odor of man, the trampled areas serving as attractions to fly, which thus unduly increase in numbers. For this reason, the quantitative catching is done at some distance, the site being shielded from the physical stations by means of large grass screens placed in echelon.

⁵ Density plus activity has been used by the Nigerian investigators ('27, p. 429) in much the same sense.

Upon the catching site, every possible effort is made to avoid trampling of paths and impregnation of these with human odor. An apparently satisfactory method is to set out a series of parallel lines, from 10 to 25 yards apart, these lines being divided into 25-yard subsections. According to program, these subsections are visited once per week only, the disturbing effects of the catching party being thus reduced to the minimum.

Before approaching these "grids," the party "de-flies" itself—that is, removes all following fly, places these in tubes, deposits the tubes upon the de-flying site, and on return from the "grid," arranges for the release of these fly by one man, the main party by this time being out of range.

Upon the catching line, the party—consisting of a uniform number of uniformly clad catchers—after recording for 1 minute the degree of liveliness and desire of the fly to bite, traverses the 25 yard distance in 5 minutes, by alternate movements and halts. The flies captured are recorded by minutes. The details of station, hour, date, and degree of "hunger" are recorded upon the thorax of each fly by means of a systematized series of oil-paint dots. My colleague, Mr. Scott ('31), has described a most valuable method of marking insects by means of paint.

During the time of catch, light-intensity, humidity, temperature, and rate of wind, are measured by portable equipment.

(ii) Mechanical Traps

Mechanical traps have been found of little use in tsetse work, but at least one type, that of Harris ('30), is worthy of development. The only types that need be recorded are these of Harris ('30), Balfour ('12, p. 10; '13, p. 118) and Shircore ('16).

Balfour's trap, made by the Andrea Maire Company, resembles the large cotton moth traps made by the same company. Balfour has suggested that the central strands or wicks should be soaked in such materials as water and human sweat, or citrated blood, and that possibly a living animal might be placed within the trap. No data are available as regards efficiency, but it is exceedingly doubtful if the fly would be attracted at all or, any rate, in numbers likely to be of any value in quantitative work.

Shircore's trap consists of a series of revolving canvas screen-vanes, upon which adhesives are spread. The object of the wind-driven vanes is to attract the attention of *G. morsitans*, that of the adhesive to capture the fly. A modification of this trap is to be tried shortly. It will consist of a series of screens rotated at a given rate by means of a mechanical device worked by a boy hidden in a shelter at a distance from the catching site. For quantitative work, it is essential that the vanes always rotate at the same speed. No adhesives will be used, but instead a uniform catching party armed with nets.

Harris ('30) has described an excellent tsetse-fly trap which I have recently seen doing most efficient work in Zululand, with *Glossina pallidipes*. Without attempting to go into the details of construction of this trap, I would

say that, altogether apart from its possible great utility in reducing the numbers of tsetse, it presents an excellent collecting device for the animal ecologist *working with insects attracted by optic stimuli*.

Based upon the knowledge that the tsetse hunts by *sight* to a greater degree than by scent, the trap presents the following features attractive to the tsetse—and to other Diptera such as Tabanids: (i) bulk—the trap is a box about 6 feet x 3 x 2½ ft; (ii) symmetry—in end view the trap simulates the end view of an animal—it tapers from top to bottom; (iii) color—its walls are of *khaki* hessian; white walls render the trap much less attractive; black walls cause the fly to settle *outside* the trap instead of entering it; (iv) slight motion—the trap hangs from stout wires, and is moved slightly to and fro by air currents; in some instances Harris has provided tags of hessian at the ends of the trap, which blow in the wind and simulate the moving ears or tail of an animal; (v) *contrasts of light-values*, this being the most important point of all—the trap casts a shadow upon the ground (it is hung 6 to 18 inches above ground level, or vegetation level), has at its bottom a narrow slit (from 2 inches to 2 feet wide) running its whole length, while at the top of the trap a slit allows the access of day-light to the otherwise relatively dark chamber.

The trap works in this wise: fly is attracted to the trap by the various features mentioned; it is especially attracted by light-value contrasts to the shadow below the trap. When in the shadow, its primary optic instinct to respond to light conditions other than those it is experiencing, forces it to fly toward the source of strong white light appearing through the slit at the top of the trap, and visible to the fly through the long, narrow slit at the bottom of the trap, just above the shadow cast by the trap. The fly enters the large, relatively dark chamber formed by the hessian walls and the wooden roof; it does not remain in this chamber for more than a few seconds, but proceeds *volens volens* to the slit at the roof. Above this slit is an ordinary lobster-pot-principle, one-way house-fly trap. In this gauze chamber captured flies collect. In quantitative work the trap could be exposed within a given site or community for a standard time, and the number of fly collected in that time determined. To provide against death of the fly from insolation, the gauze cage would be provided with a *partial*, white, semi-transparent roof.

The point of great interest is that Harris has shown that about one year's collecting has produced about 82% female tsetse. As female tsetse normally are most difficult to collect by man or animal bait methods, this point is of fundamental importance. Equally interesting, Harris finds that modifications of the trap, or of nature of exposure of the trap, have some influence, little understood, upon the proportion of male flies captured.

This valuable means of obtaining samples is being steadily studied and improved by its industrious and capable inventor.

Students especially interested in the capture of blood-feeding, sight-hunting insects are advised to consult Harris' own report. This trap has been patented by the inventor.

I have attempted to use this trap, experimentally, with *G. morsitans*. For this species the trap requires special modification.

(iii) Liming or the Use of Adhesives

Considerable use has been made in practice of skin or cloth smeared with bird-lime or other adhesive, and carried on the backs of natives. The use of such in quantitative work, however, is to be deprecated, for the reason that the adhesives cause death to most of the fly caught.

(iv) Bait

In certain instances it is desirable to utilize bait cattle to draw out female fly and fly not so hungry as to desire to attack man. This is done by driving or leading several cattle through the area under investigation, the human party being kept to the minimum practicable for herding and catching purposes. Tethered animals have not proved very successful, owing to their usually not presenting sufficient movement.

It has been attempted to attract tsetse-fly by means of animal bladders filled with blood, and slung upon the backs of natives. Owing to the variation in the appeal of the bait according to age, wind, temperature, and hunger of the fly, the method has little value in quantitative studies.

4. GRANARY INSECTS

Insects in granaries may be attracted by water according to the method of Dendy and Elkington ('20), the visiting insects being captured by adhesives or by water traps on the lobster-pot principle. Owing to the death of the insects, these methods are inferior to the simple taking of a unit volume of grain by means of a suitably shaped scoop, and the counting of the insects therein. Sample and insects should be returned to the site.

5. BIRDS

Apart from ordinary censuses of birds, extremely little has been done as regards the study of bird numbers. No method is entirely satisfactory, but the more suitable are as follows:

(i) To count the number of nests at breeding seasons, and from this calculate the probable numbers of birds. It is to be remembered, however, that non-breeding individuals are entirely disregarded by this method.

(ii) To observe the birds along a given length and width of transect, preferably within a given period of time. This method has been employed successfully by Forbes ('07) by Forbes and Gross ('22), and by Grinnell and Storer ('24), but it seems that while Forbes worked upon an area basis, Grinnell and Storer worked upon a *time* basis. Undoubtedly the better method is to utilize both length of transect and time as bases. Within dense vegetation the method is less difficult than it is in open, as some cover is

afforded the observer, while the lateral range of his inspection perforce is limited. A difficulty is the inspection of birds in very high trees. In open communities birds are more liable to take to flight.

(iii) An excellent method is for the observer to hide among natural cover, and to observe within a definite time the number of birds of different species that appear within a definite radius.

(iv) In Africa, "bird-lime," made of a mixture of tree *Euphorbia* latex, rosin (colophony) and raw linseed oil, is useful for smaller birds that frequent shrubs and trees. Either special rods or the twigs and foliage of the trees and shrubs themselves may be spread with this effective adhesive. There are some useful "bird-limes" upon the market, of which "Ratsticker" is a good example. Ground birds may be caught by spreading "bird-lime" upon flat boards of definite size, and then sprinkling litter lightly over this, finally adding a little adhesive to the upper parts of the litter. In this work, unit surface and unit time, again, should be the basis of the observations.

(v) When one particular species of bird is to be studied, and if a knowledge of its habits be possessed, the employment of suitable decoys, or traps on the "bait-lever-and-door" principle, sometimes yield satisfactory information. This is particularly true in the instance of ground birds.

6. SMALLER VERTEBRATES

In practice, the smaller vertebrates are largely rodents and other mammals, but of course include the reptiles and amphibians. Despite the large amount of useful work done upon rodents and other small animals by the Biological Survey of the United States and by investigators in Russia and Mongolia, the literature of methods of determining the numbers of small animals is very meager. Apart from trapping, poisoning, and shooting—all of which are essentially unsatisfactory from the viewpoint of the student of animal numbers—the sole methods so far applied appear to be these of direct observation, and the enumeration of the number of lairs upon definite areas. By means of the last-named method it is possible to determine roughly the numbers by means of direct counts of animals within 5 per cent of the numbers of lairs, and by calculation therefrom. In endeavoring to count the animals within the sample lairs, care must be taken beforehand to close all exit holes, otherwise entirely fallacious results will follow.

7. LARGER VERTEBRATES

Literature on counting larger vertebrates there is almost none.

In a country such as East Africa, where large mammals not only are exceedingly abundant but play an important part in the ecology of the biotic community, it is essential to have some method of periodic determination of numbers. Methods that may be employed with reasonable success are:

(i) Transects may be traversed through selected vegetation types, upon

these transects animals seen to right and left of the observer at a given distance being recorded. With some species of animal this method is highly successful, but with the more timid it is entirely useless. On account of the poor visibility it has little value in dense vegetation. Unit time and unit area should be the bases.

Shelford ('29, p. 39) has suggested a useful modification of the simple transect method—that of first distributing a known number of domesticated animals within the area to be observed. The actual number of stock seen is noted, as well as the actual number of wild animals. From these data, the supposed proportion of game not visible is determined by simple calculation. Obviously this is fraught with many errors, but the extent of these may be determined to some degree when the habits of the animal under study are known.

(ii) Where cover for an observer is good, and if the vegetation be not too dense, the observation upon a time basis, of a unit area of which the site sheltering the observer is the center, has many advantages.

(iii) Daily recording of the kind and the abundance of "spoor" at drinking holes, or upon unit area in grazing grounds, is possible, provided the "spoor" is marked daily by means of sand, chalk, ochre, small metal tags, or other suitable materials. Lime, salt, bone, and such like materials are to be avoided as they not only are removed by game but also are attractants in country where alkalis are lacking. Sharp river sand may be sprinkled upon unit areas, "spoor" upon these observed, the surface daily being re-smoothed.

(iv) The driving of coyotes (see Shelford, '29, p. 40), jackals, hares, and other animals, supplies data of doubtful value. I have known parties of men and trained dogs hunting areas known to harbor many jackals, succeed in driving either no or very few animals in a day. Hares, on the other hand, may be started comparatively readily.

8. PARASITES OF PLANTS AND ANIMALS

Animals parasitic upon the various organs of plants, usually may be determined by means of transects or analysis circles set out in the vegetation. In the case of parasites of fruits, it is usual to determine by direct examination the number of animals within a large number of fruits, and then to apply this proportionally to the total fruit crop.

Ectoparasites of animals, especially the less mobile forms, are most readily determined by the basis of the number per unit area.

Conclusion

In the foregoing account, my statement that all too little as to the study of animal numbers is known, and that the field is still held by methods the most empirical, is emphasized. That this outline may serve as a stimulus to greater effort being exerted in a field of such far-reaching importance is my hope.

I again urge the necessity of studying not only numbers, but also habits, associated plants, and animals, and the physical habitat.

Summary

1. It is necessary to improve our information as to animal numbers and the variation in such numbers, should we wish to add appreciably to our knowledge of the basic interrelations of plants and animals in biotic communities.

2. Very little is known as to the more suitable methods to apply to an investigation of variations in numbers. An attempt is made to bring together the views of various workers, and to make such suggestions as have arisen as the results of the writer's own experience in field ecology.

3. A consideration of the methods is given according to some of the more important types of animals.

4. It is suggested that investigation in this field would provide interesting and important work for biologists.

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POLLEN ANALYSIS OF MUD LAKE BOG IN OHIO¹

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Mud Lake Bog surrounds a small pond lying on Lat. 40° 40' N., near Long. 82° 9' W. and within a few miles of the edge of the late Wisconsin drift. The area is partly in Sections 26-27, Washington Township, Holmes County, partly in Sections 22-23, Lake Township, Ashland County, Ohio. It lies between Wooster and Loudonville, close to the intersections of state routes Nos. 3 and 179.

Mud Lake is one of a series of small lakes lying in a wide drift-filled valley now traversed by Lake Fork of the Mohican River, a tributary of the Ohio River system. The lake surface has an elevation of 940 feet, while the tops of the nearby hills reach 1,100. There is evidence that the water level was formerly higher, and the water area greater than at present.

In contrast to this, the Bucyrus Bog, described in a previous paper (Sears, '30), lies in a shallow depression on the Ohio-Erie watershed, at an elevation of 1,040 feet. It appears to have been forming peat during early post-glacial time while Mud Lake was very slowly depositing silt and marl. Its more recent deposits have been injured by oxidation during dry periods, by erosion, and by recent fires. Mud Lake, on the other hand, appears to have been forming peat continuously during recent times. Thus the two deposits are in a sense complementary. Details of the early post-glacial coniferous period appear *in extenso* in the Bucyrus Bog, those of more recent deciduous time in the Mud Lake deposits.

The vegetation of Mud Lake Bog has been described briefly by Dachnowski ('12). After a lapse of 18 years there appears no need to modify his account. Unfortunately the vegetation of other peat areas in Ohio has not been so well conserved. The same author discussed the peat, mentioning its generally low ash content.

Samples of the peat were taken and prepared as described in a previous paper (Sears, '30). The ones reported on here were all taken at 6 inch intervals excepting for the two lowest samples which were a foot apart. Because of the slow rate of silting when the lowest deposits were formed, this gives a somewhat telescoped record of the earliest strata, but those above have yielded a clear and connected story. For most strata, over 250 pollen grains per foot were counted and identified, but in the lowest layer fossils were too scarce to permit this. Erdtman ('21) shows that 100 to 150 grains give a good indication of the percentages of the more abundant pollen kinds, and

¹ Contributions from the Botanical Laboratory, University of Oklahoma, N. S. No. 8.

TABLE I. *Mud Lake Bog. Percentages of fossil pollen at one foot intervals*

Depth in feet		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Conifers																										
	Abies.....	003	004	01	003	05	02	01	02	06	02	04	04	09	06	004	10	01	02		01	01	01	015	01	04
	Larix.....				003			003		004					004									01	01	85
	Picea.....	04	044	07	063	014	05	01	013	02	04	03	03	04	04	01	03	054	03	04	02	01	01	01	01	15
	Pinus.....			01	01							01							01	003	004	01	01	01	02	
	Tsuga.....																									
Dicots																										
	Acer.....	03	03	06	02	04	03	03	05	02	03	03	03	01	02	01	004	04	02	01			003			
	Anacanth-Chen.			01					003											01	004					
	Betulaceae.....	08	05	04	06	054	04	04	043	04	034	004	023	014	004	01	024	008	01	013	02	023	05	015	02	
	Carya.....	09	06	09	11	16	17	17	15	22	23	31	30	26	27	22	18	21	14	12	09	21	16	18	26	
	Castalia.....	01	01	01	01	01	01	003			004		003		004	004	01		01			01	003			
	Compositae.....	04	01		01	01		003																		
	Ericaceae.....																									
	Fagus.....	06	04	03	04	01	01	003	04	004	02	02	02	03	03	04	04	02	08	10	22	17	10	05	07	
	Fraxinus.....						003												003				003			
	Juglans.....	02		01	01	01	01	02	01	01	01			03	004	02	02	05	03	04	10	03	003			
	Populus.....		01																							
	Quercus.....	52	57	59	54	57	53	58	51	47	53	46	47	44	44	48	42	49	47	46	39	40	50	51	27	
	Salix.....																			01	01	01	02			
	Tilia.....	003			003	004	03	02	03	02	004	004	01	02	02	004	01	02	05	07	05	06	04	02	07	
	Ulmus.....	03	01		01	004																				
Monocots																										
	Cyperaceae.....	003	01					01		01																
	Gramineae.....	01	01	01	003	004	02	02	01	02	03	01	01	01	02	01	02	02	02	01	02	003	01	01		
	Juncus.....																									
	Potamogeton.....						003	003	003											003			003			
	Sagittaria.....		004																							
	Typha.....				01					004										003			003			
	Unknown.....	06	13	08	10	08	08	07	12	11	06	084	06	06	07	04	11	08	114	103	06	07	07	05		
	Pollen counted.....	264	270	158	280	253	292	288	282	232	276	250	309	283	247	273	241	255	258	348	267	327	322	200	117	46
	Pollen frequency.....	129	91	117	94	144	85	92	116	65	118	75	115	120	108	119	52	111	154	174	192	210	290	152	58	36
Peat.....		Dark fibrous.....Dark green fibrous.....Dark green oozy.....Shelly.....																								

my own experience agrees. Bowman ('31), however, has recently advanced reasons for counting at least 1,000 grains from each level.

The statistics obtained are set forth in Table I. Calculations have been made to the nearest percentage, but where less than 1 per cent is present, the decimal is given. The table also gives number of grains counted for each level, pollen frequency, and character of peat.

Table II presents suggestions as to the climatic significance of the kinds of pollen found, and serves as a key to the chart, figure 1, in which percentages are distributed according to their possible significance. It will of course be understood that the terms used to designate moisture and temperature conditions are necessarily personal and relative, based upon experience in the middle western United States. Approximately, conditions north of the Great Lakes would be "cool," south, "warm," east of them, "moist," west, "dry."

TABLE II. *Mud Lake Bog. Suggested climatic significance of pollen found*

Moisture	Temperature		
	"Cool"	Uncertain	"Warm"
"Moist"	Abies Larix Tsuga	Castalia Salix Cyperaceae Juncus Potamogeton Sagittaria Typha	Acer Fagus Juglans Tilia Ulmus
Uncertain	Picea	Ericaceae Populus Unknown Betulaceae	Fraxinus Quercus
"Dry"	Pinus	Gramineae	Amaranthaceae Carya Compositae

Table I shows a predominance of fir, with spruce, at the lowest level. This agrees with the record of the Bucyrus Bog. The details of change to the oak-hickory-pine maximum in the 24-foot level are missing, probably for reasons already noted, but will doubtless appear with closer sampling. At the 20-foot level a brief but definite maximum for beach and walnut appears, with a minimum for hickory and oak. Above this there is a prolonged dominance of oak and hickory, culminating at the 11-foot level, above which other species slowly become more important.

The climatic conditions inferred from these facts are set forth in fig. 1.

Any value the diagram, fig. 1, may have rests upon three assumptions: first, that the proportions of pollen found by the methods used are substantially correct; second, that, if correct they give a reasonable—not by any

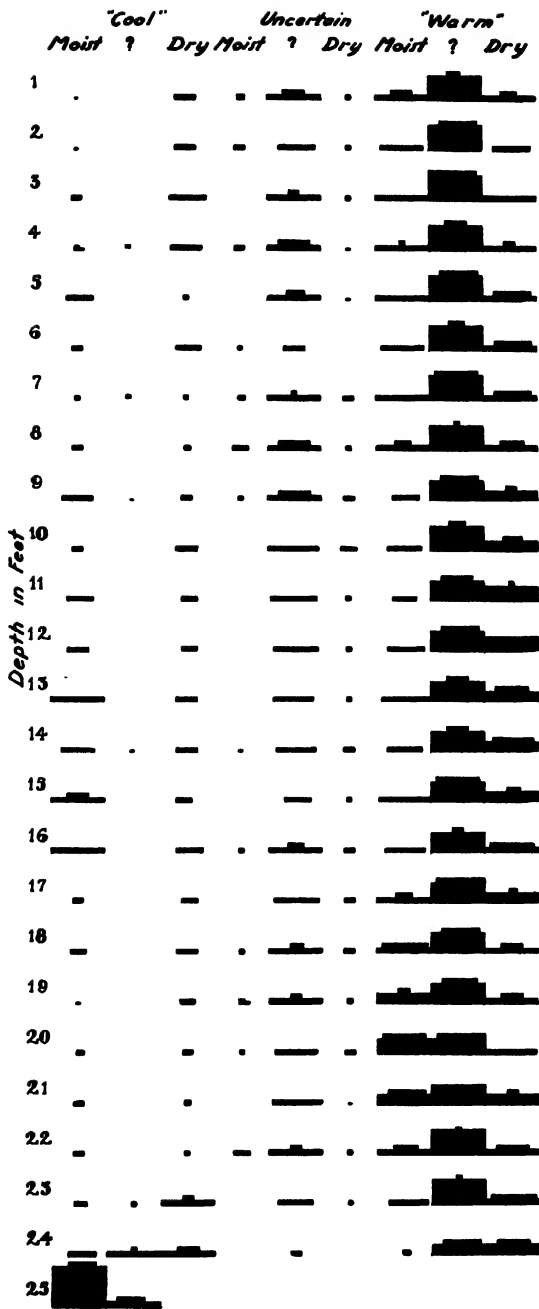


FIG. 1. Pollen analysis of Mud Lake Bog in Ohio. Distribution of fossil pollen at each foot of level according to probable climatic significance (cf. Table II). Three major columns indicate temperature conditions, with moisture conditions under each. Note predominance of warm dry indicators from 5th to 18th foot; warm moist from 18th to 21st; and dry conditions by beginning of 24th foot. Record of 25th foot is telescoped here—for details of cool period see Sears, '30, also discussion in text.

means a complete—idea of the regional vegetation at successive times; third, that the significance of the various genera or families is approximately that indicated by the classification in Table II. All three assumptions are subject to a certain amount of experimental checking, and such checking is one of the urgent problems of pollen analysis.

The striking feature of the diagram is the nearly complete shift from cool indicators to warm ones above the 25-foot level. That this was not so abrupt as it seems here appears from the analysis of the Bucyrus Bog, already discussed (p. 650). From the 24-foot level up the alternation of dry and wet indicators is the principal phenomenon shown.

Evidence that the cool coniferous period ended in a dry wave is afforded by the transition from coniferous to deciduous conditions in the 24th and 23rd feet. The balance here is in favor of dry indicators.

A humid fluctuation is strongly suggested by conditions from the 22nd through the 18th foot. The climax of this is at the 20th foot. Above this, warm dry indicators predominate through the 4th foot. Their climax appears about the 11th foot. The upper 3 feet show a decrease of the dry indicators, giving a fair balance of wet and dry under the warm columns.

There appears to be no serious discrepancy between the moisture fluctuations of the warm columns, and those of the center columns which list forms whose temperature significance is not clear.

Under the cool columns however, there are some apparent discrepancies, notably from the 16th through the 9th foot, and the 5th through the 1st. In general it should be remembered that cool indicators in a warm climate occupy selected habitats, in which the effect of moisture shifts might not register concurrently with their effect on more generalized habitats. The "humid" conifers of the 16 to 9 foot levels are largely larch—a tree which invades filled or perhaps, drying, bogs. In the latter event, its abundance at these levels would be no real discrepancy. In the upper levels the "dry" conifer is pine, unquestionably *Pinus strobus*. The Mud Lake Bog lies within the range of the white pine and at least 40 miles north of the range limits of the southern xerophytic pines—*P. virginiana* and *P. rigida*. Here again the discrepancy may be apparent rather than real, since *P. strobus* is the most mesophytic of the pines of the region.

The extended record for deciduous forest climate which this bog reveals is matched in other bogs sampled since the Bucyrus Bog (Sears, '30) was described. The upper 2 feet only of the latter are predominantly deciduous. During the dry season just past, this deposit was examined by digging, and evidence obtained that fire, erosion and oxidation had been more generally active in the layers above the coniferous than was realized at the time the report was published.

Certain inferences therefore of the earlier paper must now be revised, notably the idea that deciduous forest time has been brief, and humid throughout. The conclusion that the Ohio climate is now warmer than it has ever

been since Wisconsin glaciation is no longer tenable in view of the evidence from Mud Lake, and a second, warm, continental maximum must be admitted as a probability in addition to the cool continental maximum indicated by the evidence of the previous paper.

SUMMARY

The pollen analysis of Mud Lake Bog, northeast of central Ohio, gives an extended record of the changes of adjacent vegetation after the disappearance of a predominantly coniferous forest from the region.

It thus supplements the detailed record of coniferous forest conditions shown by the Bucyrus Bog (Sears, '30). The combined records now suggest 2 dry periods in postglacial time—the first cool, toward the end of coniferous time, and the second warm, occupying most of deciduous time. Two humid periods are indicated in the past—cool, at the beginning of coniferous time and moderate, early in deciduous time,—while the present trend seems to be towards more humid conditions. Such descriptive terms are of course purely relative.

The characteristic fossil pollen flora of the deposit is as follows: *Abies-Picea*—25th foot; *Pinus-Carya-Quercus*—24th foot; *Fagus-Juglans-Quercus*—20th foot; *Carya-Quercus*—11th–12th foot; *Quercus* and mixed mesophytic—1st and 2nd foot.

Acknowledgments are due the National Research Council, Doctor W. B. Bizzell and Professor H. H. Bartlett. Mr. Fred Tinney assisted in collecting material from this and numerous other bogs, and with Miss Mabel Larcomb prepared the material for study.

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NOTES ON THE LOUISIANA CONCH, *THAIS HAEMASTOMA* LINN., IN ITS RELATION TO THE OYSTER, *OSTREA VIRGINICA*

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In this paper, the writer will attempt to discuss some important points in the biology of *Thais haemastoma*, and to indicate the positions occupied by these points in the interrelationship between the conch, *Thais*, and the Louisiana oyster, *Ostrea virginica*. This interrelationship is considered mainly from an economic point of view, *i.e.*, the aspect of interest to the oyster industry. The only published accounts of this species of *Thais* are some fragmentary observations included in the oyster surveys of Moore ('13 a, '13 b), Moore and Danglede ('15), and Moore and Pope ('10). Federighi ('30) has published a short account of the Atlantic coast oyster drill, *Urosalpinx*, a snail which seems to occupy somewhat the same niche there that *Thais haemastoma* does in Louisiana. Colton ('16) gives a brief account of the life-history of *Thais lapilla*, which has been reported to attack oysters along the North Atlantic coast.

OYSTER PRODUCING AREAS OF LOUISIANA

The oyster-producing areas of the Louisiana coastal waters are mostly shallow, mud or oyster-shell bottomed, land-locked bays. Two main regions may be discerned in the productive area here under consideration, that centred about the Mississippi River drainage: (1) The bottoms east of the Mississippi River. The water here is of low salinity during much of the year. The oyster reefs are of natural growth, the bivalves being densely clustered, and covered with the abundant spat. In many places mussels (*Mytilus clava* Meuschen) are attached to the oysters in great numbers. Conchs are rare, although they have been reported to sometimes become abundant for brief periods. (2) The bottoms west of the Mississippi. The water here is of fairly high salinity. Great freshets occur occasionally, however, as after the breaking of the river levees. At the present time the oysters here are almost all in cultivated beds, which, in many localities, must be planted with seed oysters brought from other regions, because of the early death of the naturally attaching spat. Mussels are not abundant. Conchs are numerous.

CONCH'S METHOD OF FEEDING ON OYSTERS

Thais haemastoma is a prosobranchiate gastropod (Fig. 1). It attains a length of 75 mm., although it becomes sexually mature at smaller sizes. In

common with many of its relatives, this species feeds on bivalves, drilling a neat round hole through the shell (Fig. 2), and extracting the flesh through this hole by means of an extensible proboscis. In Louisiana, this borer is regarded as one of the important enemies of the oyster. Counts of the freshly drilled shells of oysters, made in the latter part of August, 1930, indicated that a large number of oysters of marketable size, and an even larger

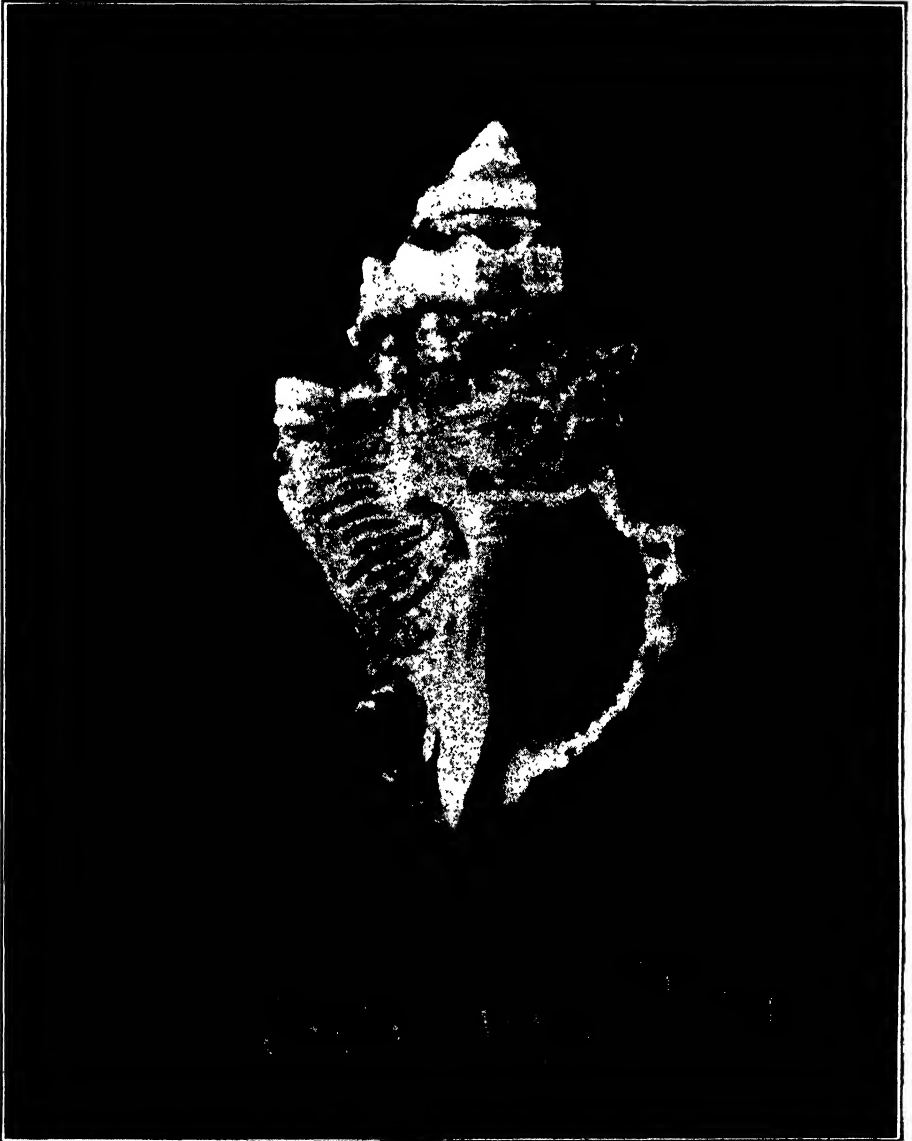


FIG. 1. Above. Adult *Thais haemastoma*, $\times 2$. Below. A cluster of egg-capsules of *T. haemastoma*, $\times 2$. Photographs from preserved material.

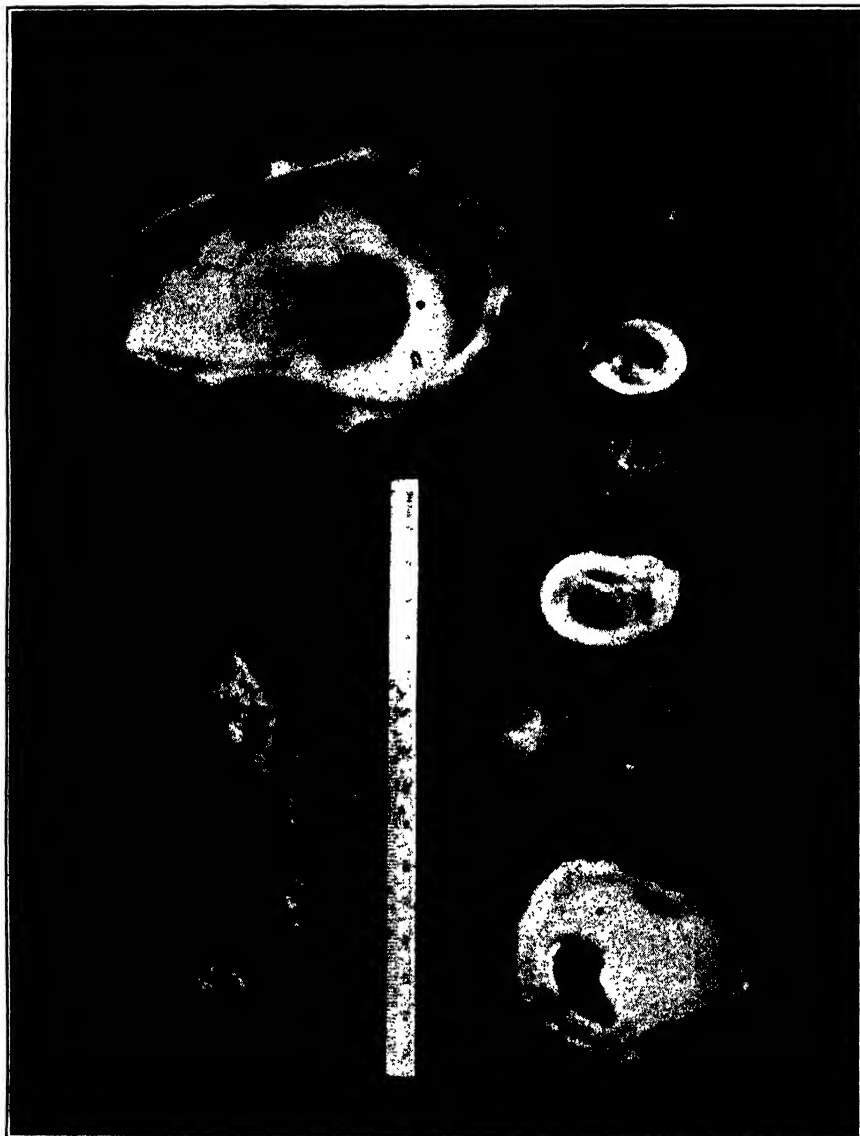


FIG. 2. Conch-killed oysters, showing the holes drilled in the shells by *Thais*.

number of smaller oysters, had been killed by *Thais*. The animal seems to begin to feed actively at the end of its spawning season, in June, as no freshly drilled shells¹ were found before that time. It apparently does not kill many oysters during the cold weather. Observations on the conchs of a shallow water reef have led the writer to believe that the shell of an attacked oyster is drilled through rather rapidly, probably in less than 12 hours, and that there is no very long rest period after each meal. The fatal hole may be drilled through any part of the shell, but field observations indicate that at least half of the shells are pierced at their ventral edge, where the valves make contact. The hole is therefore often a hardly apparent semicircle in the thin, projecting periostracum of each valve. Since the periostracum of the empty shell rapidly weathers away a short time after the death of the oyster, it soon becomes impossible to tell that an edge-drilled shell was emptied by a conch. Thus it is probable that the shells of at least half of the conch-killed oysters of a reef do not indicate the manner of death, and no exact field estimate can be made of the number of oysters killed by conchs. Owing partially to the doubt thus set up as to the exact status of the drill as an oyster enemy, little coördinated effort at its control has been made. After the hole has been drilled, the soft parts of the still-living oyster are eaten. Since the adductor muscle is eaten last, the valves of the shell remain closed until the flesh is completely devoured. Many of the animals associated with the oyster reefs are readily attracted to oyster flesh, so that the fact that the shell remains closed undoubtedly allows the borer to complete its meal without competition.

RELATION OF OYSTERS AND MUSSELS TO CONCHS

While the oyster forms the chief food of *Thais*, experiments and observations indicate that the conch will eat mussels (*Mytilus clava*) in preference to oysters, if they are procurable. In regions where conchs are numerous, mussels are very rare, while in localities not infested with borers, mussels are often so numerous as to cover the oysters. Besides the competition for food and space set up between the two bivalves in such localities, the clustering mussels make it economically undesirable to fish such oysters, owing to the difficulty of culling them clean. Thus natural oyster reefs heavily overgrown with mussels are removed both from the beneficial effect of the breaking up and scattering of the crowded clumps by man, and the injurious possibility of overfishing. In addition, in such localities the range of the oyster is not extended over barren bottoms by the establishment of man-made beds.

The limiting factor in the distribution of the mussel has been usually considered to be salinity, since mussels may be abundant in waters of low mean salinity, while they are rare in waters of high mean salinity. How-

¹ Those empty shells whose two valves were still held in place by the hinge ligament were considered to be freshly dead.

ever, in regions of high salinity, in a certain few small areas of bottom, in which drills were rare, mussels were observed to be rather abundant. On other, neighboring patches of reef, where drills were common, the only mussels to be found were a few small individuals wedged deep in the protecting clefts between groups of oysters; numerous drilled shells of mussels were found in the bottom mud of these areas. (The shells of mussels do not remain attached to the byssus after the death of the animal, but fall to the the bottom.) Of oysters and mussels confined in live-cars with borers, the mussels were always eaten before the oysters were attacked. It therefore seems probable that the mussel is limited to regions of low salinity, not because it cannot endure high salinities, but because it is preyed upon too extensively by the borer in the regions of high salinity favorable to the growth of the latter. *Thais* is limited in its distribution to areas of fairly constant high salinity, apparently directly, by salinity. In regions where the snail is usually abundant, freshets may temporarily exterminate it, while it is never found in places regularly subject to incursions of fresh water.

SIZE OF OYSTERS PREFERRED BY CONCHS

The borer appears to prefer small oysters to larger ones. Evidence obtained from counts of the conch-drilled shells gathered from infested oyster reefs, and from observations on feeding conchs both in nature and confined in live-cars with oysters of various sizes, indicates that oysters of given sizes are eaten in numbers inversely proportional to size. No clear correspondence could be found between the size of the borer and the size of the oyster attacked, but from the diameter of the holes drilled in large shells taken from the reef, it seems likely that small conchs do not attack oysters of the largest sizes. The result of this selective removal of small oysters seems to be that reefs infested with borers are able to maintain themselves under natural conditions, but are likely to be exterminated by the drain of large individuals induced by oyster-fishing. It is interesting to note that on the east side of the river where conchs rarely occur, the natural reefs appear to be holding their own, in spite of intensive fishing operations, while to the west of the river where conchs are abundant, the formerly present natural reefs have been exterminated. Areas west of the river which contained only the oysters planted there by man, have, after a freshet which exterminated the borer, produced quantities of spat which survived to maturity. Such areas have thus been made profitable again as natural fisheries, but with the recovery of the borer and the resumption of fishing operations, these reestablished natural beds are rapidly disappearing. New generations of oysters are produced in fair abundance in these areas, but most of them seem to be devoured by the conch before they reach a marketable size. Conchs may have a partly beneficial effect, from the standpoint of the oyster planter, on cultivated oyster beds or those planted with seed oysters, by preventing the growth of cluster-

ing young, which make culling more difficult. The fishermen report that the snail or "bigorneau" appears to attack large oysters more extensively when small oysters are not present. It is interesting to note, as an addition to the extensive powers of selection possessed by *Thais*, that no borers were ever observed to drill the abundant empty oyster shells, although the external surfaces of these cannot be seen to differ from those of living oysters. Borers resting on dead oyster shells were often observed to have cleared away small patches of algae.

BREEDING HABITS OF THE CONCH AND METHOD OF CONTROL

The breeding season of *Thais* is in April and May, although a few eggs have been found as late as the end of July. While breeding, there seems to be a massing of conchs in large numbers in limited portions of the infested reefs. In connection with this, it may be noted that adult snails, in August, were observed to be capable of moving about a foot in five minutes, which seems fairly rapid; the movements at this season, however, appear to be of small extent. The animals were able to progress even over very soft muddy bottom. Fishermen report that oysters in the areas in which the conchs have congregated are poisoned or smothered by the mass of snails, but the author has not yet enough data to link the snails with such wholesale destruction.

The conchs develop a tendency, for the breeding period only, to climb as high as possible (below low tide mark) on structures elevated above the surrounding bottoms. The eggs are fastened to these elevated objects, thereby preventing their being smothered by debris or silt. Because of this habit, the animals can be trapped during the breeding season. Stakes with bunches of palmetto leaves wired to them are erected throughout the area to be trapped; the animals, climbing up, accumulate on the trap. The conchs which have climbed these traps are removed at intervals by pulling up the stake and shaking it over the bottom of the collector's boat; the writer estimates that he has seen 5,000 conchs removed from traps set over an area about 100 yards square, at a single visit.

The eggs, embedded in a gelatinous matrix, are enclosed in horny transparent capsules about 10 mm. in length. These capsules are attached to the substrate about 1 mm. apart, their bases being joined by a common sheet of the capsule substance. Each capsule contains about 1,000 eggs, and a female produces 100 or more capsules. The writer estimates that he has seen capsules representing 10,000,000 eggs attached to a single trap. These attached eggs may be killed by drying the stake for a few hours, which, however, is not usually done. Owing to the enclosed yolky eggs, fresh-laid capsules have a creamy color, which soon darkens to brown as debris accumulates on the external surface. Capsules whose contained eggs or larvae have died take on a reddish purple color similar to that produced by the secretion of the

anal glands of the adult (Tyrian purple). The length of the period before hatching is probably at least 2 weeks, since luxuriant hydroid colonies may be found on capsules still containing larvae.

The larvae are hatched as veligers, escaping from the capsule through the hole left by the loss of a minute operculum in its truncate distal end. The larvae of *Thais haemastoma* do not seem to be reduced in number, as those of *T. lapilla* are reported to be, by cannibalism during the encapsuled period. They pass through a free-swimming period of unknown duration, during which they may be found abundantly in the surface tow and are probably then widely disseminated. The veligers sink to the bottom in perfectly still water, but do not attach themselves. A slight agitation of the water of their container is sufficient to keep them afloat, with the aid of their vigorous ciliary action. The food of these planktonic larvae has not been determined.

It is probable that the greatest mortality among borers occurs during this free-swimming stage, as few of the egg-capsules have been found in nature with their contents destroyed, and the only factor destructive to the adult, aside from physico-chemical conditions, seems to be man. A locality in which the adults have been reduced in number through trapping or a temporary invasion of fresh water, is repopulated by larvae drifting in from neighboring untrapped or permanently salty areas. Federighi ('30) finds that the larvae, few in number, of *Urosalpinx*, do not go through a free-swimming stage. Owing to the limited migratory powers of the adult, he believes that vigorous trapping will permanently remove this snail from an isolated oyster bed. In Louisiana, owing to the enormous areas of uncultivated bottoms over which *Thais* occurs, in which it is economically impossible to reduce the number of animals by trapping, there is a constant reservoir of breeding conchs whose free swimming larvae quickly obliterate the effects of localized trapping. Thus trapping over a limited area must be repeated at each breeding season, and the only result of trapping a bedding ground from year to year is the prevention of the accumulation of drills, which appear to reach maturity in one year. The only system of control possible for Louisiana waters would seem to be an economic one: the development of a market value of some sort for the trapped animals, which would reimburse the oyster-planter for the expense of yearly trapping by the sale of his catch.²

DISTRIBUTION OF THE CONCH, AND FACTORS AFFECTING IT

Thais is very variable in abundance and distribution, both from place to place, and in the same place from season to season. It is probable that a shifting complex of such factors as salinity, temperature, available food, tide-currents (for transportation of the free-swimming larvae), powers of locomotion of the adult, character of the bottom, and efforts at control by man, is

² The conch is considered edible by many people of the State, but is rarely offered in the markets.

responsible for this variation. At present, salinity, or some factor associated with it, seems to be the most powerful limiting factor. The oyster is capable of surviving a much lower salinity than the conch, hence part of its range is not overlapped by that of the snail. Permanent changes in the drainage of the land, brought about by man, no doubt have caused and are causing extensive shifts in the range and numbers of the borer.

EARLIER OBSERVATIONS

Moore has concluded that the snail destroys young oysters in numbers great enough to render cultivation of naturally attaching spat difficult in regions of high salinity where borers are numerous. A number of the observations of Moore on *Thais* (*Purpura*) *haemastoma* are not in accord with those of the writer. Some of these statements are repeated by Churchill ('20). The following statements by Moore and his associates may be discussed: Moore ('13, b, pp. 33-34), writes "The drill or whelk lays its eggs in red or purple leathery capsules. . . ." The writer notes that the capsules are creamy when laid, and only turn "red or purple" on the death of the contained embryos.

"The young become destructive to the minute spat immediately on emerging from the egg cases. . . ." The writer finds that a free-swimming period intervenes before any possible destruction of young spat, unless Moore refers to planktonic oyster larvae.

"After the shell is perforated the proboscis is thrust into the shell and the contents eaten, other drills sometimes partaking of the feast by entering the gaping shell of the dead or dying oyster." The writer notes that in all cases he has observed, the still-functioning adductor muscle of the oyster is eaten last, the shell thus necessarily remaining closed until the solitary "feast" is completed.

Moore and Pope ('10, pp. 23-24, 51), say "Each capsule contains several eggs, and the snails escape through holes . . . which they cut in the free end of the capsule." "Several" must here be taken to mean approximately a thousand. The "hole" in the free end of the capsule is left by the loss of an operculum whose presence is indicated, by an excavated ring, from the time the capsule is laid. It is unlikely that the minute veligers cut this operculum free.

"Seed oysters 2 inches or possibly not less than 1½ inches long appear to be immune [from the borer]." While it is true that many more small than large oysters are killed by the borer, the writer finds that commercially appreciable numbers of the latter are killed, and that no size of oyster is immune from the borer.

SUMMARY

1. The chief food of *Thais haemastoma* is the oyster (*Ostrea virginica*). Small oysters are preferred to large ones. Thus, large numbers of oysters.

both of marketable size, and of the new generation are destroyed each year by the borer. The selective destruction of young oysters seems to result in the extinction of the oysters of reefs which, previously in equilibrium with the drill, are subjected by fishing operations to a drain of the large individuals.

2. *Thais* prefers mussels (*Mytilus clava*) to oysters as food, and seems to prevent mussels from becoming abundant in regions where the borer flourishes. Thus, oysters exposed to the attacks of the drill are partially compensated for their reduction in number by their freedom from the presence of the mussel; on the other hand, the presence of mussels undoubtedly diminishes the number of oysters eaten.

3. *Thais* seems to be unable to live in waters whose salinity is low. Its range thus does not completely coincide with that of the oyster and mussel.

4. During the breeding season, *Thais* displays a strong negative geotropism. Its numbers in such limited areas as planted oyster beds can thus be reduced by yearly trapping.

5. *Thais* produces very large numbers of larvae, which pass through a free-swimming stage. It is therefore a very difficult animal to control, both in range and in numbers, by any method economically possible.

The writer wishes to thank the Smithsonian Institute, which identified the borer and the mussel, and supplied a note on the literature. He wishes to express his indebtedness to the several oyster fishermen, who permitted the use of their oyster-boats, -beds, and -camps, and supplied a number of observations; to Dr. E. S. Hathaway of Tulane University, who read and criticized the manuscript; to the personnel of the Department of Conservation, and to others who have aided him.

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THE PERIOD OF HEIGHT GROWTH IN SOME NORTH-EASTERN CONIFERS¹

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INTRODUCTION

In studying the reactions caused in plant communities either by the plants themselves or by external agencies, it is of interest and value to follow as closely as possible the phenomena of growth under various conditions. Especially is this true of forest vegetation where growth is of so great commercial importance. In the present instance attention has been directed to certain conifers, which, because of their present importance to the paper and pulp industry, it is most desired to perpetuate in the forests under consideration.

Tree growth may be observed and measured in many forms. In the earlier stages of development height growth suggests itself as convenient to measure, and, in degree as the species is sensitive in response, is an excellent indicator of the effect of different treatments, such as release cuttings, trenchings, etc. In other words, individual plants may be measured to determine the growth rate of that species of plant under the given conditions, or the plants may be considered in the nature of phytometers, indicating quantitatively the effect of external factors. Specifically, height growth in the seedling stage often determines whether or not a young tree will be able to survive and outstrip competitors of the same and other species. Competition for growing space is particularly intense among the invading vegetation following such severe disturbances as fire and lumbering. Like the time of germination, the period during which height growth takes place each season may have an important bearing on the ability of a species to attain dominance. In any investigation involving the growth of forest trees, such as a study of volume increment, whether by permanent or temporary sample plots, it is of importance to take the necessary measurements at a time when growth is not in progress. This presupposes a knowledge of when such growth takes place. Seeding, planting and transplanting operations should also be timed with regard to the natural period of growth (Watson, '20). The times of beginning and ending growth may also be significant in the choice of seed of local races for planting in a different region. Again, the seasonal habits of certain insects seem to be correlated with the course of height growth of the trees they attack. A knowledge of the latter may be of value in the

¹ Presented in original form before the Ecological Society of America at Philadelphia, Pennsylvania, December 28, 1926.

adoption of control measures. Tendencies brought out in a comprehensive study of the course of seasonal growth might throw light on other problems not considered at the start. Ultimately the scope of the investigation might be enlarged to include the many factors which are involved. That the present paper does not attempt to do; it is in the nature more of a preliminary report, and summarizes merely the results of four season's observations—data too meagre for drawing definite conclusions. It is presented at this time rather in the hope of enlisting the interest of plant physiologists, ecologists, foresters and others in making similar measurements in other localities and thus providing material for regional studies of wider scope and application.

OBJECTS AND SCOPE OF THE INVESTIGATION

The original purpose of the investigation was to determine the course of seasonal elongation of the terminal growing shoot, its rate at different periods, and the dates of starting and stopping growth in the species selected for study. Furthermore it was hoped to discover the effect on the above of the following factors: 1. Density of cover, aspect, forest type, soil type, etc. 2. Soil and air temperature and other climatic factors. 3. Height, age and growing conditions of the tree measured. 4. Altitude and latitude (indirectly climatic factors).

It was also planned to compare the rates of growth of the various species under the same and different conditions. Not all these factors will be considered in the present paper. It is planned to treat them more fully in a later communication.

The present observations were made in the years 1925, 1926 and 1927 at Cupsuptic Lake, Oquossoc, Maine, and in 1926, 1927, 1928 at Berlin, New Hampshire. Additional observations were made at the Harvard Forest, Petersham, Massachusetts, in 1927 and 1928 on northern white pine (*Pinus strobus*) by Dr. Harvey J. MacAloney. Prof. J. Nelson Spaeth kindly co-operated by making measurements of white and red pine (*Pinus resinosa*) at Ithaca, New York, in 1927. Daily measurements during July, 1927 on Mt. Desert Island, Maine, made by Mr. K. A. Salman were kindly supplied by Mr. H. B. Peirson of the Maine Forest Service. Usually measurements were made weekly on the same day throughout the season. In all, over 9,830 measurements of current growth were taken, in addition to other data on each tree.

HISTORICAL

No attempt at an exhaustive survey of the literature will be made here, because fairly complete bibliographies have been published by Romell ('25), Burger ('26), and Hertz ('29). A few more important European investigations will be mentioned, as well as American studies on the species dealt with in this paper.

The seasonal course of height growth of the principal European species

has been studied repeatedly, and a wealth of material is available especially on Scotch pine (*Pinus sylvestris*) and Norway spruce (*Picea excelsa*). Tolsky ('13), from 4 years' observations in Russia, found that in the Province of Samara the height growth of *Pinus sylvestris* took place in May and June. The needles continued to grow in July and August. A gradual, uniform development of shoots took place, varying with the weather. On cold nights in May the growth ceased entirely. Day growth was greater than night in May, while the reverse was true in June. A correlation between the amount of elongation and the weather of the previous year was noted, the growth varying in direct proportion to temperature and precipitation. However, weather conditions of the year at the start of growth were important. Klebs ('14) investigated beech (*Fagus sylvatica*) in Germany. He emphasized the importance of food supplies in controlling the growth period. He concluded that a rest period was not essential; that the relative supply of carbohydrates to the growing points determined growth or rest. Light was considered important in its effect on the food supply. Kübler ('10) also concluded that the growth of young shoots depended mainly upon reserve materials of the previous year. Burger ('26) compiled the results of investigation carried on since 1898 by the Swiss Forest Experiment Station at Zürich. Over 194,000 measurements were taken. He concluded that the amount of any one year's growth is largely dependent on the amount of reserve food stored during the previous growing season, and therefore on the weather of that year. On the other hand, the course of growth is influenced by the temperature of the year, without, however, any direct correlation except regarding duration. Burger's results agree in the main with the findings of Romell ('25) for Sweden. The latter observed a retardation in the starting of growth of Scotch pine due to differences in latitude and altitude; in Norway spruce no such tendencies were observed. The course of growth of the latter species seemed to be governed largely by local weather conditions. Whether or not the trees were shaded by an overwood had little effect on the dates of starting growth. Hiley and Cunliffe ('22) arrived at similar conclusions, as did Wallén ('17). In more recent work the importance of light—the so-called photoperiod—in controlling the time of growth, especially its ceasing has been pointed out. Amilon ('19) found the culmination of height growth occurred earlier in light demanding trees. Dostal ('27), in his attempts at forcing, found the photoperiod effective.

In America some fragmentary information exists on the time of starting and stopping height growth. Hastings ('03) studied chiefly the period of cambial activity, but mentions that white pine buds were just opening on May 19th. A considerable body of phenological observations of this nature has been collected. Brown ('12, '15) studied the course of growth in pitch pine (*Pinus rigida*) and white pine. The latter had begun elongation of the leader on May 3, 1913 at Ithaca, New York; 50 trees were measured. Growth began the last of April and continued until July 4th. Elongation

of needles continued until August 15th. The daily increment was 1.2 to 1.9 per cent. It was concluded that temperature was the primary factor starting growth, since food and moisture were at the optimum. Illick ('19) reported the results of daily measurements on 200 trees in Pennsylvania during 4 seasons. White pine and Norway spruce ceased growth by July 1st: 90 per cent of the elongation took place in less than 90 days, twice as much at night as during the day; 39 per cent of the growth took place in the day in white pine, only 18 per cent in the Norway spruce. The date of starting growth in Norway spruce depended on the origin of the seed. In another publication Illick ('23) states that most of the growth takes place within a month.

Pearson ('18) found moisture of more importance than temperature in regions of low precipitation. In a later paper ('24) he records 14 years' observations on western yellow pine (*Pinus ponderosa scopulorum*). Growth began the middle of May in Arizona, was most rapid in June, and was complete by July 1st. He also noted needle growth until into August. The major part of height growth took place in the driest month of the year. The similarity of the season here recorded with that in very different species in widely different climates is very striking, suggesting the importance of light. Gail ('26) found that the osmotic pressure of western yellow pine (*Pinus ponderosa*) and lowland white fir (*Abies grandis*) increased in summer after mid-July, indicating "that growth ceases by the middle of July." Thereafter photosynthesis continues and storage exceeds consumption, thus causing a rise of osmotic pressure. He thought the drought during July, August and September might inhibit growth. Nakashima ('29) has recently studied Austrian pine (*Pinus nigra* var. *Austriaca*) with recording apparatus: 91 per cent of the growth took place between May 21 and July 19. During this period evaporation was of greatest importance of any meteorological factor in influencing the rate of growth.

Lamb ('15) gives in a chart the broad limits for leaving in balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), and white pine, but does not indicate the course of height growth. Moore ('17) appears to have been one of the first to study red spruce (*Picea rubra*) and balsam fir. He gives the end of the growing season as August 19th for the former and July 10th for the latter. In a study on Mt. Desert Island, Maine, Moore ('19) found the following dates: *Abies balsamea* started June 1, ceased July 10; *Picea rubra* and *Pinus strobus*, June 5 to August 20. He pointed out that the dates averaged 15 days later than found by Nachtigall ('16) in Germany. Balsam fir grew faster and formed new needles sooner than red spruce. The length of the growing period seemed to be influenced considerably by the character of the soil. Thus when seedlings were transplanted, a second growth ("Johannistrieb") was begun in the following cases: raw humus, 38 per cent; mild humus, 11 per cent; mineral soil, 9 per cent.

Marie-Victorin ('27) gives the time for starting growth in red spruce

as toward the end of May in Southern Quebec. He notes that growth starts later in black spruce (*Picea mariana*). In white pine he states that growth extends over $5\frac{1}{2}$ months. The annual shoot begins toward the beginning of May and ceases the 1st of August. Needles grow two or more weeks longer. Rees ('29) observed the shoot elongation of red spruce in the Adirondacks in connection with a study of diameter growth. Leaf buds did not burst until the middle of June in 1927 at Cranberry Lake, New York, and growth was complete by the last of July. A slight secondary elongation of the leader was noticed. Slight differences in time of growth were found in different forest types.

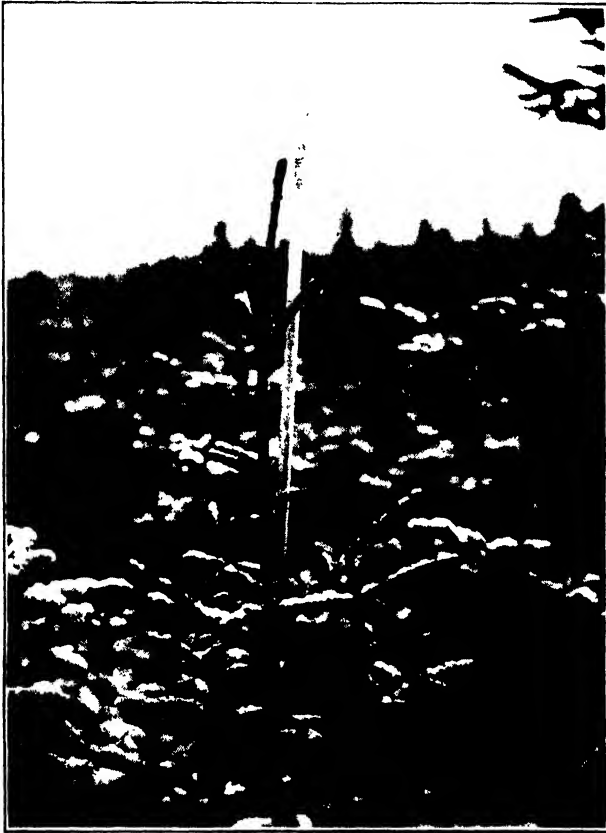


FIG. 1. Method of attaching scale to tree.

Studies throughout the north temperate zone have shown quite consistently that height growth in conifers takes place during a comparatively short period, with a maximum about the time of greatest length of day. Fluctuations in rate and date of starting appear dependent upon the weather of the year, specifically temperature where that is limiting. The total amount

of growth has been correlated with the food reserves available depending on the weather of the previous year.

METHODS AND NUMBER AND LOCATION OF TREES MEASURED

To insure the measurements being taken from the same point each time, a light lath was attached to each tree in such a manner that it could not slip. Ordinary building lath free from knots were planed and split lengthwise so as to form sticks approximately $1 \times .5$ cm. in cross section and 1 m. long. The sticks were tied to the trees with soft cotton string or tape and prevented from slipping by cutting notches where they met branches. About .5 m. was left to project above the terminal bud. The sticks were in every case



FIG. 2. Method of measurement.

attached to the north sides of the trees so as not to shade the growing tip (Fig. 1). The starting point or zero of this improvised scale was taken as the tip of the bud before growth started; this point was not only marked in pencil, but cut into the wood with a knife. Measurements were made by

sighting horizontally across the top of the bud (to avoid parallax) and marking the position on the stick by a fine horizontal line, using a sharp, hard pencil. The distance between this mark and the starting scratch was then measured with a thin steel rule graduated in mm. (A Lufkin No. 2200 ME 30 cm. long was found convenient for this purpose) (Fig. 2). Each stick was numbered, and measurements were recorded, when made, in a notebook opposite the tree number. At the end of the season all sticks were collected and the marked distance checked against those recorded in the notebook. Measurements were made on the same day each week, and as far as possible at the same time of day, beginning about May 1st and continuing until September 1st. When attaching the scale the following data were recorded for each tree: species; total height; length of each of the last three whorls of the top in mm.; forest type, age, etc.; soil and moisture conditions; character and density of overhead cover; exposure (direction slope faced;) absolute and relative elevation.

The above description may seem unnecessarily detailed for such a simple apparatus, but it developed that extreme care was necessary to obtain complete sets of weekly readings. Of the 80 trees originally set up in 1925, almost one-half suffered from accidents of one sort or another so that the records were rendered incomplete, and had to be discarded in the averaging. Frosting back of the terminal bud was a common cause; injury by animals, wind and breakage of the sticks, or failure to relocate the tree when the leaves became dense, were other causes. Of the complete sets of measurements secured, 23 were of red spruce, 2 white spruce, 9 black spruce, and 22 of balsam fir. This experience indicated that a sufficient number of trees should be measured to allow for accidents. The superiority of periodic observation with simple apparatus of this kind, over auxographs and other recording instruments, however desirable for some purposes, lies in making practical the measurement of a large number of trees, and thus overcoming individual variations.

In 1925, 80 trees varying in height from .2 meter to 5 meters and situated in a variety of conditions, near Cupsuptic Lake, Maine, were selected for observation. Balsam fir, red spruce, white spruce, and black spruce were included. The essential part of the field observations was the measurement of the length of the growing tip at weekly intervals.

In 1926, 40 trees were measured on one site at Cupsuptic Lake and 25 at Berlin, New Hampshire. The latter were distributed equally beneath hardwood sprouts and in an adjacent opening. In 1927 it was possible to measure only 17 trees at Cupsuptic Lake, and 75 at Berlin. During this season, 50 trees were measured at Petersham, Massachusetts, 42 at Ithaca and 25 at Mt. Desert Island. In 1928, 75 trees were measured at Berlin and 150 at Petersham. In all cases a certain number of trees had to be discarded because of frost injury or other accident.

METEOROLOGICAL OBSERVATIONS

In 1925 at Cupsuptic Lake, soil temperature observations were made on 5 of the different situations where trees were being measured. Air temperature was also recorded at the central station up to July 1st, after which the station had to be discontinued. During succeeding years it was not possible to follow temperatures in the field, and data from the nearest meteorological station were substituted.

The soil thermometers were exposed as follows: A piece of wood $7 \times 7 \times 40$ cm. was drilled to within 10 cm. of the end, making a hollow tube with a 2.5 cm. hole. The undrilled end was then sharpened for ease in inserting in the ground, and two small drain holes were bored, slanting from the sharpened end in to the central hole. The outside point of these holes was set exactly one foot beneath the surface of the soil, the object being that the temperature of the soil could be freely communicated to the thermometer bulb through these holes. That portion of the tube destined to be beneath the ground was coated with tar; the rest was painted white, as was a wooden cover carrying a cork, to which the thermometer was attached by a short copper wire. A plain 25 cm. nitrogen-filled chemical thermometer was used. The bulb was protected by a small cork, and the thermometer adjusted to hang with the bulb opposite the drain holes. This method of exposure of soil thermometers is believed to be superior to the so-called standard soil thermometer used in agricultural work, and is a modification of that described by Bates and Zon ('22). Comparison with several thermometers exposed in a large soil well after the manner of Toumey and Stickel ('25) indicated that thermometers in the well at the same depth read only $\frac{1}{2}$ degree F. lower. Connell ('23) has recommended iron pipes, but, while they are convenient to make and resist decay, they have little advantage over wood.

Before installation, each thermometer was calibrated by comparison with a corrected thermometer, and corrections attached to the thermometers by tags. As the range of temperatures recorded was so slight, a single correction was sufficient. Unfortunately, maximum and minimum thermometers were not available. Readings of the soil thermometers were made twice daily at 6 A.M. and 6 P.M. at the central station (Station 1), and at weekly intervals at the others. The record for Station 1 extends from April 16th to July 1st; for the others from May 10th to August 23d. Soil temperature data are given in Table 1.

Since air temperature records had to be discontinued on July 1st on account of pressure of other work elsewhere, the daily means for Rumford, Maine, the nearest Weather Bureau station, were computed and plotted along with those taken at Cupsuptic Lake. The trends of the two curves were sufficiently similar to justify the substitution of the Rumford temperatures when analyzing the growth variations during July and August. Mean² daily

² The mean was taken as the morning reading plus the evening reading divided by 2.

TABLE I. Weekly mean soil temperature at 30 cm., 1925. Degrees F. Cuscutpic Lake, Maine

Station	April 26	May					June					July				August		
		3	10	17	24	31	7	14	21	28	5	12	19	26	2	9	16	23
1. Cutover spruce flat	28	26	34	39	40	41	50	48	49	49					59	58	58	56
2. Uncut virgin hdw., N. slope			38	40	42	44	48	48	48	48	50	52	54	55	54	58	58	56
3. Cutover virgin hdw., N. slope			40	41	42	45	50	50	50	50	51	58	58	56	58	58	57	57
4. Cutover virgin hdw., S. slope			46	42	45	52	55	52	52	51	53	54	59	57	59	59	59	57
5. Uncut virgin hdw., S. slope															60	59	58	57
Average	28	26	39	40	41	45	50	49	48	50	51	52	58	56	58	58	58	56

For descriptions of stations see Table II.

air temperatures for Rumford and Cupsuptic Lake—were plotted adjacent to the curves for height growth.

At Berlin, records of the Weather Bureau cooperative station, located 0.5 km. from where the trees were measured, were used.

For Petersham, temperature and rainfall records made on the Harvard Forest near the trees measured, were supplied through the courtesy of Mr. Paul W. Stickel of the Northeastern Forest Experiment Station.

For the Ithaca station records were obtained from the local Weather Bureau located about 1.2 km. from the plantations.

MEASUREMENTS

The study was first carried out on forest lands surrounding Cupsuptic Lake in northwestern Maine. The topography is rolling and seldom precipitous. The altitude of the lake is about 450 m. above sea level, and the mountains rise 300–600 m. higher. All trees measured were confined to the lower slopes or flats about the lake (for description of stations see Table II). The underlying rock consists of a highly metamorphosed schist, and the soil, largely *in situ* and weathered from the rock, is a fine light yellow sandy loam. Glacial moraine is uncommon. The climate is cool, humid, with occasional spring or fall droughts, and with long snowy winters. The average growing season for crops may be taken as 120 days, but frosts may occur in any month of the year. The prevailing winds locally are from the northwest, due partly to local topography. In 1926 and 1927 trees were measured in an open clearing just northwest of the nursery. The soil in this clearing is sandy and gravelly, and somewhat drier than station 8 in 1925; also, the situation is farther from the lake, and more sheltered. The land slopes gradually toward the south.

The Berlin station was situated in the Androscoggin valley at the base of a long slope. The forest had been logged off 8 years previously, and in 1924 a weeding experiment had been carried out to remove competing hardwoods. At the time of the measurements the conifers were making rapid growth in response to the freeing. The altitude is 300 m., and the soil a rather poorly drained gravelly clay. The climate is similar to that of Cupsuptic Lake, but slightly warmer and with a longer growing season.

The Ithaca measurements of white pine were taken in a plantation 1–1.5 m. high on a 30° slope facing the northeast, at an elevation of 250 m. The red pines were but .5–1 m. high, planted on an old field in 1924. The elevation is 120 m.; 24 trees were measured.

At Petersham, trees were measured in 3 different situations. Natural white pines about 7 years old were measured on an old field. The stand was dense pure white pine, containing about 3,000 trees per acre. All trees had free overhead light. The soil is sandy loam and the altitude 300 m. The second stand measured was 6-year old (in 1927) white pine planted in blocks

TABLE II. Descriptions of stations at Cuprupt Lake

Sta. no.	Character of overwood															Characteristic ground vegetation and litter
	No. of trees used in av.*					Type†	Condition	Ap- prox. age yrs.	Den- sity (esti- mated)	Aspect	Slope	Situation	Soil	Moisture (estimate)	Direct sun received % (estimate)	
	R.S.	W.S.	B.S.	B.F.	Total											
1			8	8	16	Mixed stfw. flat	Culled	60-80	.3	Flat	0°	Sandy flat be- tween land and swamp	Fine sand	Very fresh	60	<i>Hylocomium</i> sp. <i>Chloogones hispid- ula</i> , <i>Cornus canadensis</i>
2	4				4	Spruce-hdw. slope	Virgin	0-250	.8	N	5°	Middle slope	Fine sandy loam	Very wet	1	<i>Aspidium</i> sp. <i>Viburnum alnifoli- um</i> , hardwood leaves
3	3			3	6	Spruce-hdw. slope	Cut for spruce 1923	0-250	.5	NE	5°	Middle slope	Fine sandy loam	Fresh	40	Hardwood leaves, <i>Clintonia borealis</i>
4	5			2	7	Spruce-hdw. slope	Cut for spruce 1923	0-200	.5	SW	5°	Middle slope	Fine sandy loam	Fresh	55	Hardwood leaves, <i>Rubus</i> sp.
5						Spruce-hdw. slope	Virgin	0-200	.9	NE	2°	Middle slope	Fine sandy loam	Very fresh	10	Hardwood leaves, <i>Acer spicatum</i>
6	4				4	Spruce-hdw. slope	Virgin	0-250	.9	SW	6°	Middle slope	Fine sandy loam	Moist	8	Hardwood leaves, <i>Viburnum alni- folium</i>
7	2			4	6	Paper birch slope	Followed fire. Uncut	102	1.0	Flat	0°	Rocky flat on point in lake	Very rocky loam	Fresh	2	<i>Lycopodium</i> sp. <i>Aspidium</i> sp. <i>Cornus canadensis</i>
8	5	2	1	5	13	Open pasture	Hdw. bushes kept down by grazing	0-20	.0	Sw	1°	Rocky flat on point in lake	Very rocky loam	Dry	100	<i>Hieracium aurantiacum</i> , <i>Cornus canadensis</i>
Totals..	23	2	9	22	56											

* Species indicated by initials are: R.S., red spruce; W.S., white spruce; B.S., black spruce; B.F., balsam fir.

† Abbreviations are: stfw., softwood; hdw., hardwood.

with white spruce on an old field. The cover is still largely grass. Spacing was 2×2 m., and, since the pines have grown most rapidly, they obtain full top and side light. Both these stands were measured in 1927 (47 trees) and 1928 (48 trees).

In 1928, an additional stand of planted white pine was measured. It was divided into 6 blocks containing trees from different origins; 10–20 trees were measured in each block. The trees were 7 years old when measured: 3-year stock planted in 1924. The slope is 6–8 per cent toward the west, the soil, sandy loam. In all 145 trees were measured at Petersham in 1928.

TABULATION OF RESULTS ³

The measurements of the amount of growth of the different trees on different dates show that different individuals which appeared alike in all respects, may make very different amounts of total growth during a season. These variations in total elongation have been reduced for purposes of comparison to a percentage basis, where the growth on any date is expressed as a per cent of the total seasonal growth. The percentage data were then averaged for each species and station and plotted in order to show more clearly the various relationships. In Tables III–VI are listed the dates of starting and stopping growth, length of growing season and period of most rapid growth for each species and station. Similarly, averages were reduced and curves plotted for other stations and other years. To give a better picture of the culmination of rate of height growth, the weekly increments in per cent were computed from the tables of weekly per cents of total elongation, and curves plotted (Figs. 3–5). These show graphically the differences of growth period between different species and stations.

Daily mean air temperatures were selected as data having the greatest influence upon the course of growth. These were plotted on the same horizontal scale so that they may be compared with the growth curves.

In determining the dates of starting and stopping of growth, the dates were taken on which 1 per cent and 99 per cent respectively, of the total elongation had been completed. Since measurements were made at weekly intervals, the dates are approximate only and may vary by 4 days. It was found to be very difficult to determine exactly the dates of starting and stopping growth. More significant is the period of rapid growth. This was taken as the time during which 90 per cent of the growth took place.

³ Space limitations prevent the inclusion of the measurements recorded. Copies may be obtained from the author, care Brown Co., Berlin, N. H., at cost.

TABLE III. *Dates of starting and ceasing growth, and length of period of height growth, under different conditions of cover, at Cupnupic Lake, 1925*

Sta.	Date, swelling snow cover	Date, swelling buds, all species	Date of starting growth				Date of completion of growth				Length of growing season (weeks)				Period of rapid growth								Amt. of lag behind balsam fir when 40% of the growth was completed. Days		
			Date of starting growth				Date of completion of growth				Length of growing season (weeks)				Dates				Weeks						
			B.F.	R.S.	W.S.	B.S.	B.F.	R.S.	W.S.	B.S.	B.F.	R.S.	W.S.	B.S.	B.F.	R.S.	W.S.	B.S.	R.S.	W.S.	B.S.				
1.	May 3	May 21	May 17			May 17	Aug. 9	Aug. 16	12				13	June 7 July 12	June 14 Aug. 2		June 28 Aug. 9	6					13		
2.	May 12	June 2		May 31			Aug. 9			10															
3.	Apr. 28	June 2																							
4.	Apr. 16	June 2	May 17	May 31			Aug. 2	Aug. 9		11	11			June 14 July 26	June 14 July 26			6							
5.	May 14	June 5																							
6.	May 4	June 2	May 17	May 17			Aug. 9	Aug. 2		12	11			May 31 June 21 July 12	June 21 July 26			6							
7.	May 4	May 23	May 17	May 17			Aug. 16	Aug. 23		13	14			June 14 July 26	June 14 Aug. 2	June 14 Aug. 9		7	8						
8.	Apr. 15	May 20	May 17	May 17	May 17	Aug. 16	Aug. 23	Aug. 9	Aug. 16														17		

For initials of tree species see Table II.

TABLE IV. *Dates of starting of growth. Summary for all years and stations*

Station	Year	B.F.	R.S.	W.S.	B.S.	W.P.	W.C.	Hem.
Cupsuptic Lake, Me.	1925	May 17	May 17	May 17	May 17			
Cupsuptic Lake, Me.	1926	May 31	May 31	May 24	June 7	May 24		
Cupsuptic Lake, Me.	1927	June 7		June 3		June 20		
Berlin, N. H.	1926	May 17	May 17	May 10		May 10		
Berlin, N. H.	1927	May 30	June 4			Apr. 26	May 16	
Berlin, N. H.	1928	May 26	June 15			May 14	May 19	June 11
Petersham, Mass. . .	1927					Apr. 26		
Petersham, Mass. . .	1928					May 10		
Ithaca, N. Y.	1927					May 7	(Red pine, May 4)	

Initials of tree species are: B.F., balsam fir; R.S., red spruce; W.S., white spruce; B.S., black spruce; W.P., white pine; W.C., white cedar (*Thuja occidentalis*); Hem., hemlock (*Tsuga canadensis*).

TABLE V. *Dates of ceasing growth. Summary for all years and stations*

Station	Year	B.F.	R.S.	W.S.	B.S.	W.P.	W.C.	Hem.
Cupsuptic Lake, Me.	1925	Aug. 9	Aug. 9	Aug. 9	Aug. 16			
Cupsuptic Lake, Me.	1926	Aug. 30	Aug. 23	Aug. 30	Aug. 30	Aug. 23		
Cupsuptic Lake, Me.	1927	Aug. 29		Aug. 20		Sept. 5		
Berlin, N. H.	1926	Aug. 14	Aug. 16	July 28		Aug. 9		
Berlin, N. H.	1927	Aug. 16	Aug. 15			Aug. 15	Sept. 5	
Berlin, N. H.	1928	Aug. 20	Aug. 20			Aug. 6	Aug. 20	Aug. 24
Petersham, Mass. . .	1927					Aug. 4		
Petersham, Mass. . .	1928					Aug. 16		
Ithaca, N. Y.	1927					Incomplete (Red pine, July 15)		

For tree initials see Table IV.

TABLE VI. *Length of growing season, weeks*

Station	Year	B.F.	R.S.	W.S.	B.S.	W.P.	W.C.	Hem.
Cupsuptic Lake, Me.	1925	12	11	12	13			
Cupsuptic Lake, Me.	1926	14(?)*	13(?)*	15(?)*	13(?)*	14(?)*		
Cupsuptic Lake, Me.	1927	11		11		13		
Berlin, N. H.	1926	13	15	11		13		
Berlin, N. H.	1927	11	10			16	16	
Berlin, N. H.	1928	12	10			13	13	10
Petersham, Mass.	1927					14		
Petersham, Mass.	1928					14		
Ithaca, N. Y.	1927					Incomplete (Red pine, 10 weeks)		

For tree initials see table IV.

* Record incomplete.

RESULTS

1925 Measurements

The striking fact brought out as soon as the per cents were computed was the marked similarity of the course of growth in trees whose total elongation was so different. For instance, one tree may grow 40 cm. during the season, an adjacent one but 10 cm., but on a certain date when the one tree had completed 50 per cent of its growth, the other tree would also have completed about the same proportion. The effect of shading was most apparent in a delay in the date of starting growth. Different species behaved somewhat differently in this regard, and individuals growing on cutover land in partial shade were less influenced (Fig. 3). Black spruce, however, showed little tendency to start at different times under varying conditions. No difference in the time of swelling of the buds was noticed in balsam fir on different sites, but trees of this species growing under the dense shade of paper birch made more rapid growth at the start and maintained a lead of one week over trees of the same species at Station 1, barely 75 m. distant, and growing under nearly full light, other conditions being approximately the same. Trees growing in the open made greater growth than trees suppressed in dense stands. It is reasonable to suppose that an additional one or two weeks' growing period (cf. Table III) is of considerable importance in enabling a tree to make this growth; especially is this time valuable when it comes during June when the greatest number of hours of sunlight may be utilized for assimilation. Individuals and species may be exceptions to the rule, but generally speaking it would appear that growth may start one to four weeks earlier in the open than in the forest. Any cultural operations which can cause elongation to begin earlier should prove of value in stimulating growth (see Ronge '28).

North slopes had both the latest start of growth and the shortest growing season of all sites, suggesting that heat or insolation is a factor in the growth of conifers even at this latitude and altitude.

Temperature appeared to be the most important climatic factor in determining the beginning and rapidity of height growth. It is quite probable that air temperature was equal in importance to soil temperature, or even more important; but suitable data are lacking to bring out this relation. It is believed that the first real bursting of buds occurred (on the open sites at Cupsuptic Lake) on May 20th when the air temperature reached 51° F. Rapid elongation, however, dates from June 3d or 4th when temperatures of 75° F. (23.9° C.) were reached. Following this, temperatures were again lower, since the cold water of the lake exerted a moderating influence. Sun temperatures however, were high, and for open-growing trees it is unlikely that air temperatures were again a limiting factor. From Table I and the curves for soil temperatures in figure 3 it will be noted that no appreciable growth took place until soil temperatures reached 50° F. (10° C.). On the other hand, red spruce at Station 7 began growth on May 24th when the soil

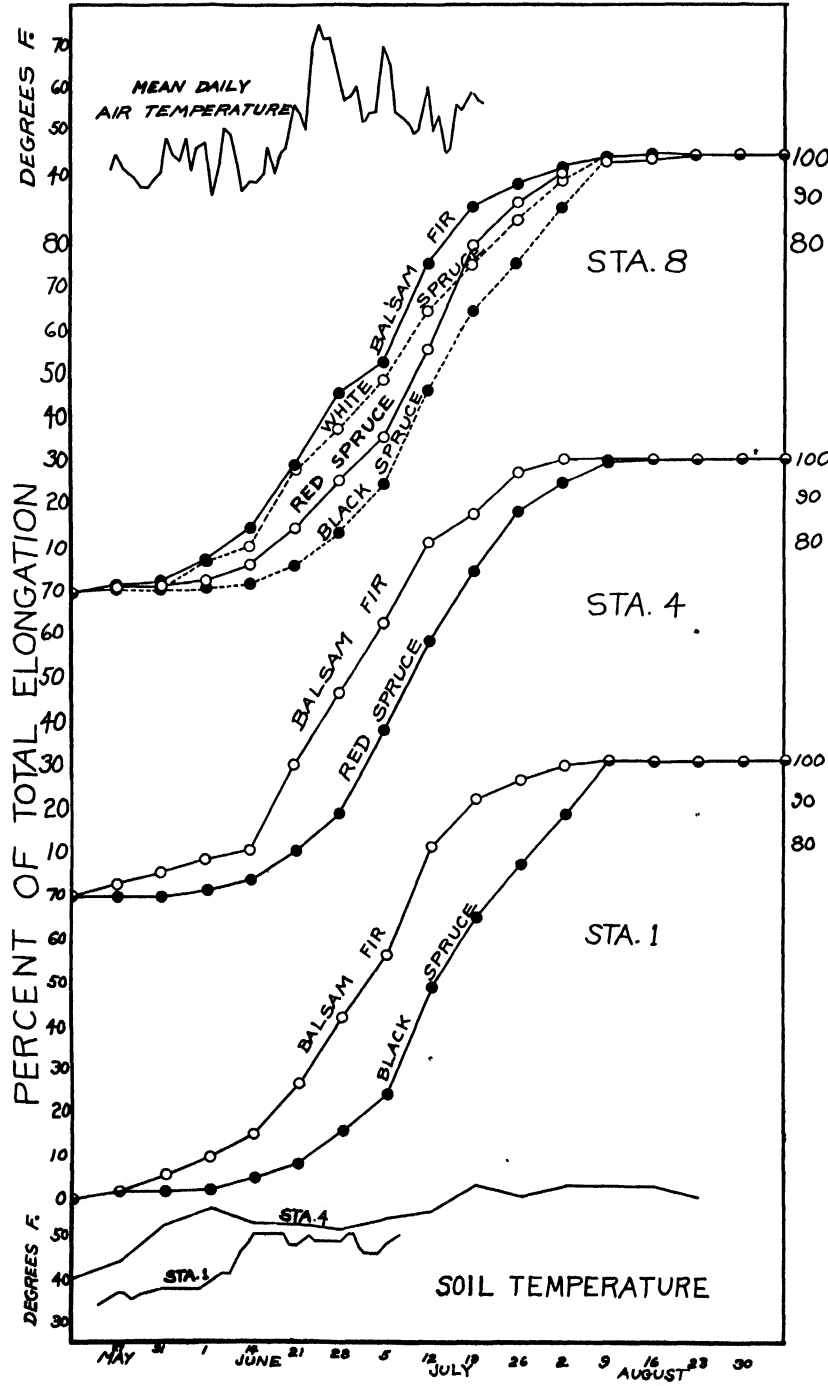


FIG. 3. Course of height growth on different sites. Cupsuptic Lake, Me. 1925.

temperature at Station 1 (the nearest soil temperature station) was but 40° F. (4.4° C.). The temperature had previously been considerably lower. Nothing further than swelling of the buds occurred until June 14th, or shortly before, when the soil temperature reached 50° F. Balsam fir on the same site continued much the same rate of growth regardless of temperature. Fifty degrees F. is only an approximate limit. Although Station 4 reached 50° by May 31st, red spruce made little or no faster progress than at colder stations. Turning again to Stations 2 and 3; red spruce began growth on June 7th in each case, but the soil temperature remained at 50° F. for the month following at Station 3 and 48° F. at Station 2.

By an inspection of the tabulated measurements, the trees of each species making the most rapid initial growth for each station were selected. With but one exception (out of 30 selections) the heights of these trees were either 2 or 3.5 m. This indicates that trees of this height, either by their success in surmounting the thickets of raspberry bushes and shrubs, or for some other reason, are in a position to make rapid height growth.

1926 Measurements

In general, the results of the previous year were confirmed in 1926. Balsam fir started growth earlier and made more rapid progress than red spruce, and red spruce surpassed black spruce. White spruce seemed to be about equal to balsam. White pine, measured this year for the first time, started and completed growth notably earlier than any of the other species.

This year it was possible to compare measurements made at Cupsuptic with those at Berlin.

The same characteristics of growth progress were exhibited by the different species at Cupsuptic and Berlin. As was expected, the Berlin trees started growth earlier than those at Cupsuptic, the advance being about 10 days on the average. The period of rapid growth was longer, often double that at Cupsuptic. While the trees at Cupsuptic continued growth later in the fall, in reality their effective rapid elongation ceased about the same time as in trees at Berlin. The difference is so small that it might easily be due to errors in measurement. In general, it would appear that increase in length of the growing season occurs by earlier starting of growth—as soon as limiting factors other than light permit; but in the fall growth ceases while climatic and edaphic factors are still favorable, giving support to the theory that the photo-period (relative length of day and night) may be the controlling factor. Dates of starting and stopping growth and length of the growing season are shown in Tables IV–VI.

But two different stations were chosen at Berlin and one at Cupsuptic. At Berlin, one station was in the open, the trees wholly unobstructed; the area had been cleared of hardwood brush in 1924 (Plot B-20). The other station was adjacent under the shade of 10-year hardwood sprouts. Here

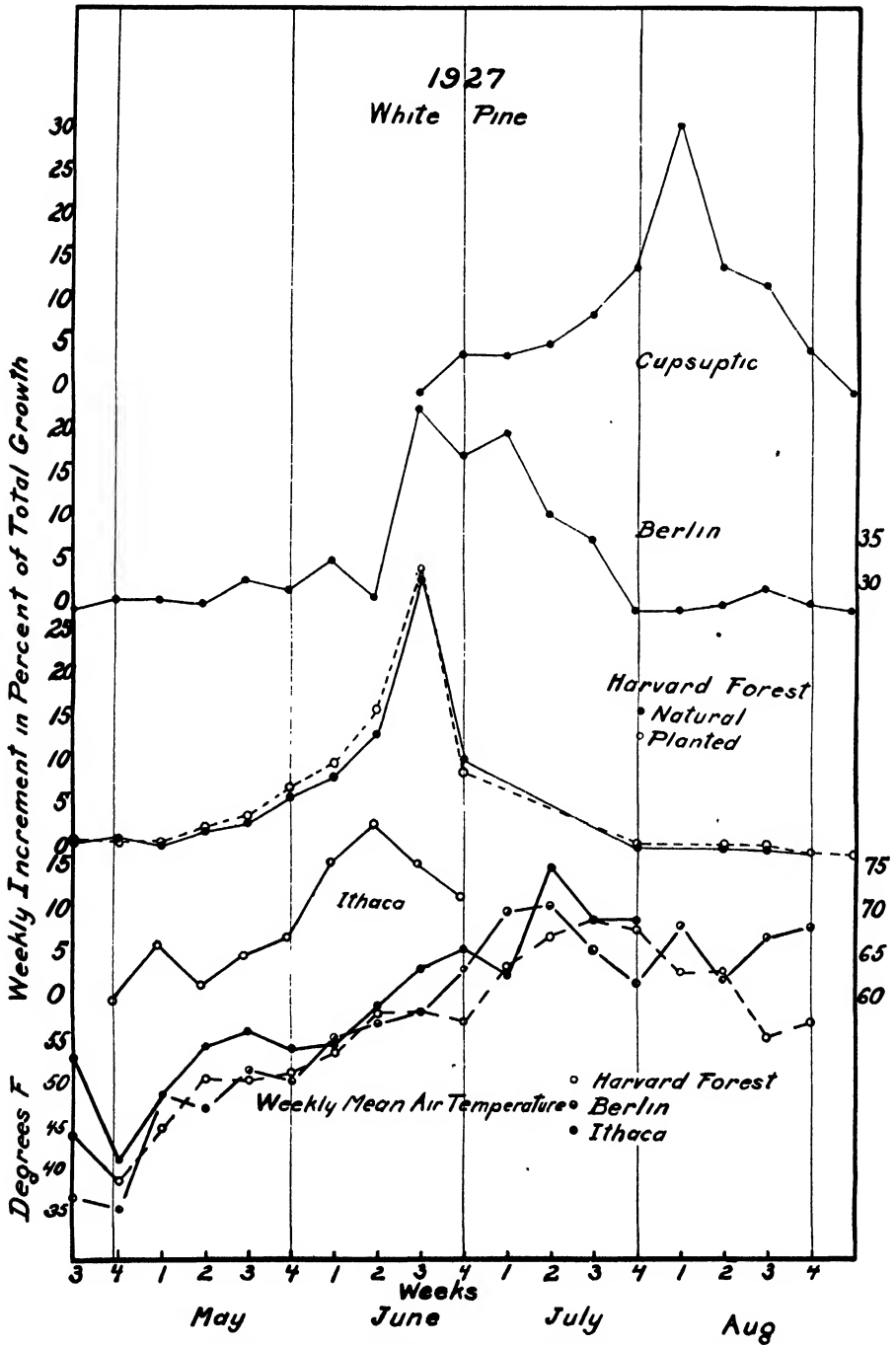


FIG. 4. Course of height growth of white pine at different places in its range, 1927.

growth started first under the shade as on Station 7, in 1925, at Cupsuptic under dense paper birch. That this is correlated to protection from cooling by nocturnal radiation seems unlikely, since all the trees which were frosted were situated under the hardwood. More probably the increased warmth from absorption by and radiation from the hardwood stems stimulated growth so early that the buds were caught by the frost. Even where frosts did not kill, they doubtless retarded growth, for the period of rapid growth for all species but pine did not start until after the last frost.

1927 Measurements

White Pine. In 1927, data were available to compare the course of growth at several different stations. For white pine growth at Cupsuptic, Berlin, Peterhasm and Ithaca can be compared in figure 4. Here it will be observed that growth began, reached its culmination and ceased at essentially the same time at the three last named places, while it was considerably later at the northernmost station. The Ithaca record is fragmentary, and the Berlin and Cupsuptic curves are based on 6 and 3 trees respectively, too few for avoiding irregularities in the shape of the curves.

Weekly means for air temperature have been plotted parallel to the curves for growth. It will be noted that the growth follows these curves fairly closely at the commencement of the growing season, but this tendency is lost before the culmination of growth is reached.

Red Spruce. Averages for Berlin show a uniform course, following weekly air temperature fluctuations rather closely up to within one week of the culmination in the third week of July. Growth began about the middle of May and was completed by the middle of August.

No significant difference could be detected between trees growing in the open and under a sprout cover.

At Mt. Desert Island, culmination occurred at the same time. Observations extended over such a short period that no conclusions can be drawn as to the dates of starting and ceasing growth. Apparently growth had ceased by the middle of August.

Balsam Fir. Growth began remarkably early at Berlin, in the first week of May, but progressed slowly until June 1st. It continued until about the first week of August when the winter buds formed (Fig. 5). As in the case of other species, the occurrence of a mean weekly air temperature of 50° F. (10° C.) and above seems to usher in the growth, but the extension of the growing season in the late summer can be explained only partly by the slightly above normal temperatures. The culmination of growth followed by one week the peak of the temperature curve. It is interesting to note that the peak of growth at Berlin coincided with a secondary maximum at Cupsuptic, the main peak of growth at the latter station coming three weeks later. That this was abnormally late for this station is suggested by the average curve

for 1925-27 (not reproduced) showing a culmination in the middle of July.

Red Pine. This species was measured only at Ithaca. Its course of growth is remarkable in following almost exactly that of white pine at the same station, including the initial rise the first week in May. The growing

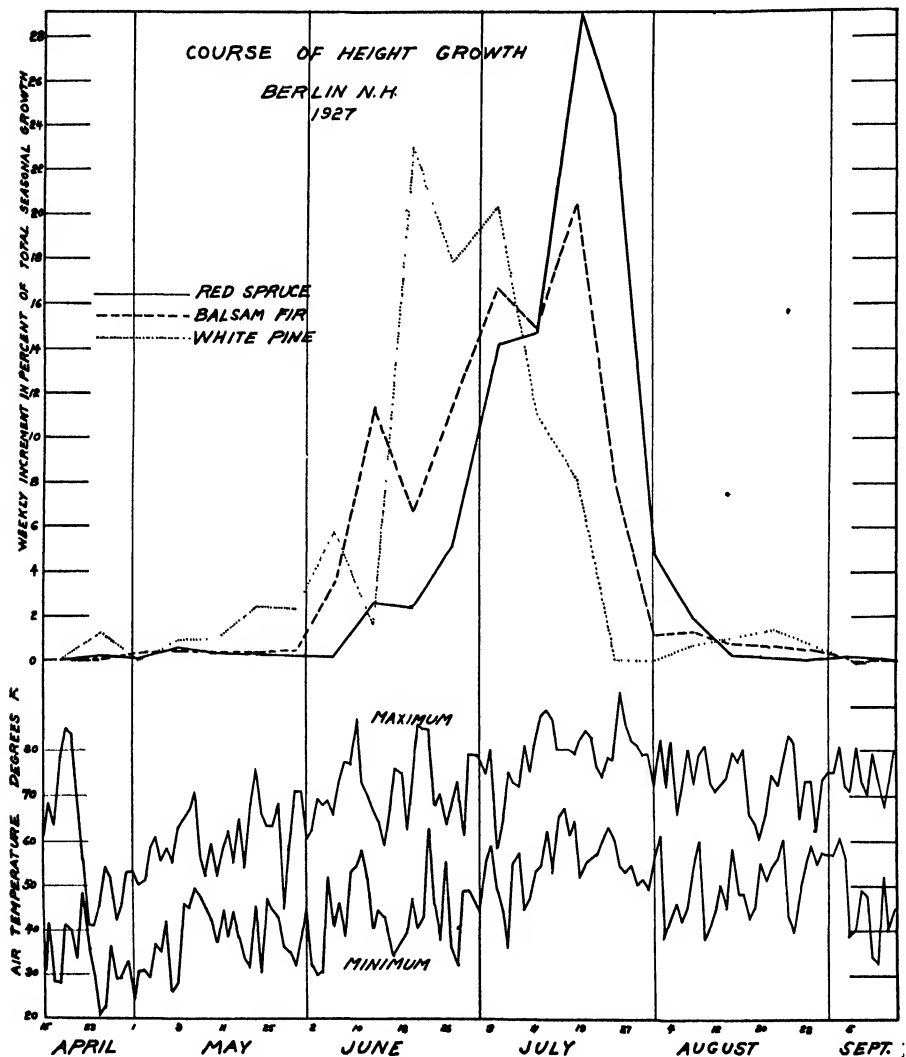


FIG. 5. Comparison of the courses of height growth of different species at Berlin, N. H., 1927.

season is shown to be from the last week in April to the second week of July, with a well-defined culmination the second week in June. Here then there was no lag with respect to the period of longest insolation, since the peak of growth occurred even before the summer solstice. This would seem

to support the theory that elongation draws chiefly on stored foods from the previous growing season, while newly assimilated products are of minor importance. Again air temperature seems to be the most potent external factor in starting growth.

COMPARISON OF DIFFERENT SPECIES

In figure 5 the courses of growth of three species growing on the same site are plotted. It will be noted that white pine started growth first, culminated and ceased elongation first, corresponding to its known promptness of response to stimuli, and more southerly range optimum. Red spruce and balsam fir paralleled each other rather closely. The latter showed greater oscillations representing responses to temperatures or other environmental factors.

1928 Measurements

White Pine. At Berlin, growth began the first week of May and was practically complete by the third week of July. The winter buds formed during the second week of August. At Petersham, natural trees also began growth the first week in May and completed it the latter part of July. The culmination was reached in both cases about the 18th to 20th of June. This coincidence of the growth at the two widely separated stations is even closer than that observed in 1927. Planted trees at Petersham began and ceased their growth at practically the same times as the natural trees, but culminated growth a week or two later (Fig. 4). A curious drop in the weekly increment can be observed in 4 of the planted stands, but not in the natural stands.

Red Spruce. Growth began remarkably late, no appreciable elongation appearing before the first week of June. Culmination occurred in the form of double maxima in the first and third weeks of July, with abrupt cessation of growth in the third week of August.

Balsam Fir. Appreciable growth began in the 2nd week of May, with culmination the first week in July and completion of growth in the third week of August. There is a curious secondary spurt the last of July, similar to that noticed in the Petersham white pine.

Northern White Cedar (Thuja occidentalis). Only 5 trees were measured. The average shows so many extreme fluctuations that it is difficult to assign a definite culmination point. Growth proceeded apparently from the 1st week of May until the last week of August.

Average Courses of Growth for the Years 1925-1928

Unweighted averages of the weekly growth increments for all the years during which observations were made on the same site have been plotted (curves not reproduced). In many respects this gives a less satisfactory picture than curves for the individual years, but yet it represents an average condition for the short period over which observations were made.

White Pine. All the curves show fairly close agreement except that for Cupsuptic which indicates a later growing season. Whether white pine requires a higher temperature to initiate height growth as compared with spruce, cannot be determined without more careful temperature observations.

Red Spruce. This species shows on the average about the same growth at Berlin and Cupsuptic. The growing season was 10 to 11 weeks long with culmination in late July.

Balsam Fir. The average curves show extreme irregularity. This is perhaps due to the balsam being more sensitive to external factors and reacting more quickly than spruce to changes in the environment. Average curves show approximately the same course for Berlin and Cupsuptic. At the latter station it shows a less pronounced culmination. A growing season of 12 to 14 weeks is indicated, with culmination in mid-July.

White Spruce and *Cedar* had a growing season about 12 and 14 weeks long respectively.

DISCUSSION

Coniferous trees differ somewhat in their courses of height growth according to their position in the forest, and according to differences in soil, shade, moisture, individual characteristics and other factors. Different species also exhibit different tendencies, which in the four conifers studied were not great. Soil and air temperature seem to determine rather frequently the date of starting of growth, but height growth stops long before these become unfavorably low in the fall. As Strasburger ('12) states: "The rise of temperature in spring is doubtless the cause of the commencement of growth but the cause of the preceding cessation of growth does not lie in lower temperature." Some other factor such as the photo-period (Garner and Allard '19, '20, '23, Lubimenko '28, McClelland '28) or drought may be the direct cause of the formation of the resting bud. The course of growth gives some insight into the characteristics of a species; thus balsam fir started and completed its growth first, in keeping with its observed greater aggressiveness and quicker response; while black spruce confirmed its reputation as a more "sluggish" species.

The relative importance of air and soil temperature could not be determined. As Romell has pointed out the weakness of the data hitherto obtained lies in the lack of coordination of air temperatures and soil temperatures. While air temperatures would seem the more influential, it is conceivable that on cold north slopes, and especially near tree line on mountains, cold soil may determine the time of growth. Bursting of the buds and elongation require an adequate water supply to maintain turgidity, such as could be possible only with roots functioning fully. On this Ronge ('28) has contributed some interesting observations.

In connection with the measurements at Petersham an interesting observation was made by MacAloney ('27) of the egg-laying habits of the white

pine weevil (*Pissodes strobi*), which seemed to correspond to the period of height growth. Weevils resumed activity at the time of swelling of the buds, and oviposition was most active about three weeks later—when rapid height growth began, confirming the findings of Graham ('18) who published a chart (p. 195) showing oviposition from April 25 to July 25 approximately.

An observation which may explain in part the slow growth of spruce and balsam reproduction noted by Zon ('03) was the high percentage of trees frosted each year. Korstian ('21) observed the same injury in his study of douglas fir. If the trees measured in the present study represent anything like average conditions, then the loss in growth from this cause may be very large in the aggregate.

SUMMARY

1. Weekly measurements of the length of the growing tip were made on a number of small conifers growing under a variety of conditions, in Maine, New Hampshire, Massachusetts and New York, during 1925, 1926, 1927 and 1928.
2. For any one species and site the proportion of growth was found to be remarkably consistent among different individuals, and independent of the total elongation.
3. Height growth of most species took place during a period of about 12 weeks.
4. The growing period was somewhat longer in the open than in the forest.
5. Fully 90 per cent of the growth took place during about 6 weeks. Growth was slow during the first month, rose rapidly to a maximum, and sank again rapidly, demonstrating clearly the grand period of growth.
6. The effect of shade was most apparent in a delay in starting growth on shaded sites. An exception was the case of a dense canopy of paper birch, where growth started earlier than elsewhere, and was maintained in vigor.
7. Trees on south slopes started growth earlier than those on north slopes.
8. Temperature seemed to be the chief determinant of the course of growth. Little growth took place until mean weekly soil and air temperatures reached 50° F. (10° C.), or until a period of warm weather had given a stimulus to all vegetation.
9. Trees about 2 m. high made the most rapid growth under the conditions studied.
10. Species differed in the rapidity of their response to factors affecting height growth, these differences being in keeping with their observed habits. Species may be arranged in the following order in relation to the time of beginning growth: northern white pine, balsam fir, white spruce, red spruce, black spruce.
11. Planted trees exhibited slightly different growth curves from natural trees, and planted trees of different origins differed from one another in the course of growth.

12. The grand period of growth in white pine corresponded to the observed season of oviposition of the white pine weevil (*Pissodes strobi*).

13. Severe damage from spring frosts was suffered by a large number of trees measured each year. This suggests that frosting back of the growing tip may be a cause of slow growth of conifer reproduction in openings.

14. The difference in time of growth of trees growing in regions of widely varying climate may be an important factor influencing the success of plantations made with stock from another region.

The writer is indebted to many cooperators for the collection and working up of the data here presented; to H. B. Peirson of the Maine Forest Service, who originally suggested the project, and supplied the data from Mt. Desert Island; to Messrs. MacAloney, Spaeth, Stickel, Hosley and Gottlieb for taking measurements and supplying meteorological data, and to E. R. Buckley, L. J. Peterson and W. E. Percival of the Brown Company for making measurements and assisting with the computations; and finally to Mr. W. R. Brown for permitting the results of the investigation to be made public.

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POLISTES WASPS AND THEIR USE OF WATER

PHIL RAU

Kirkwood, Missouri

Polistes wasps are heavy drinkers of water. From early spring until autumn they may often be seen at the water's edge or surface. The members of at least four species, *pallipes*, *annularis*, *rubiginosis* and *variatus*, have frequently been observed on the surface of the water, where, with outstretched legs, they safely alight, fill the gullets and heavily fly homeward. Often the gullet is filled to overflowing, so that a large drop in the jaws glistens conspicuously in the sunlight as the wasp wends its flight upward. Obviously, they use somehow much more than that which they consume for their own bodily needs.

I had taken it for granted that they used this water in connection with the gathering of wood pulp and the feeding of the larvae. These are probably the two main uses for the water. The habit of carrying water for these two purposes may be classified as instinctive. There is, however, another occasional activity, which I am about to describe, which ought to be classified as higher in the psychic scale than instinct.

Polistes larvae spin beautiful, white caps of silk over the openings of their paper cells. It was noticed that sometimes these caps appeared soiled and showed ripple marks, evidently left by the drying up of water. Since these marks appeared in nests well protected from rain, I suspected that for some reason or other the workers on the nest had splashed the cells with water. Hence I was not surprised when I saw this actually happening.

On July 28, 1929, I noticed the caps of many pupal cells of *P. pallipes* thoroughly wet and glistening with water. The temperature near the nest was 97° F. at the time, and I suspected that the water had been placed there for the purpose of cooling the larvae or preventing desiccation during the heat of the day.

The days of terrible heat and drought in 1930 afforded me a rare opportunity to augment these observations. The conditions were unusual enough to warrant extreme action. On these hot days of the memorable drought, the temperature in the shade often reached 103 or 105° F., while the relative humidity fell to desert conditions, 25 or 30 per cent. Only during these hot spells did we find the nests of *pallipes* drenched and dripping with water. Globules clung to the nest, both inside and outside the cells, and great, glistening drops hung quivering from the convex caps. The ground beneath was spattered with the drops which had fallen of their own weight.

On July 28, 1930, the hottest day of the year, this unusual type of activity

was practiced assiduously. The humidity was low, and the official thermometer reached 108° F., while in the flat-roofed sheds where the wasps were, it soared to 110° and 111° in the afternoon, and by 7 P.M. had dropped only to 97° . Two orphan¹ nests and one normal nest of *P. pallipes* in this shed were watched at short intervals. In these three nests, all regular work, such as cell making and food gathering for the young, was dropped for the day, and all energy was spent in trying to mitigate the heat and dryness for the young in the nests. The poor adults worked arduously all day, carrying water and constantly sousing the nests. The water-pan, ten feet away, placed there for the benefit of the *Anthophora* bees, was a busy place. Water dumped on the outside of the nest readily spread, while that inside hung in globules, sometimes threatening to overwhelm the tiny occupant. Sometimes the convex surface of a cell-cap supported a pendant drop, clear as crystal and $\frac{1}{3}$ inch long, while many of the drops grew so large that they broke of their own weight and splattered the ground beneath. Sometimes a wasp would rest on the roof of the nest for many minutes with a large drop protruding from her jaws. The normal nest had nine workers, and only a few at a time would go for water while the others would remain on the nest. In the orphan nest with only 2 adults, these alternated in getting water; as soon as one arrived with a load, the other would set out. They continued almost all day, until I wondered how their strength could endure.

On these occasions, small punctures also appeared in the lids of the cells containing immature organisms. I at first suspected that these holes had been made by young adults about to emerge. However, upon examining the cells with punctures, I found that the creatures within were in such an undeveloped stage as to preclude any possibility of their being able to use their jaws. Since these caps were always lavishly supplied with water, I concluded that these punctures had been made by the nurses for the purpose of injecting water to the inmates. I assured myself, by tasting it, that this material was not nectar or food of any sort, but just clear water.

This method of wetting the nest was practiced by the workers on orphan nests of *P. pallipes* just the same as in normal colonies. The same condition (excepting the punctures in the cell-caps) existed in the nests of *P. variatus* also.

The rapid evaporation from a nest thus drenched would reduce the temperature for the occupants by several degrees, as well as prevent their drying up in the very dry air.² In an emergency like this, where the lives of the

¹ "Orphan" nests are so designated because they are queenless nests, but contain workers, which are sometimes called nurses, and immature young. If the queen meets an accident, or if she is removed in an experiment, the nest activities go on just the same, even to the extent of egg-laying by the workers (neuter females). The eggs, however, because of their infertility, develop into males.

² It is interesting to know, according to Buxton (*Animal Life in Deserts*) that some of the desert birds adopt special methods for protecting their eggs from heat. "When one parent returns from watering, and relieves the other from duties of incubation, its

young were in danger from the unusual conditions, behavior such as this denotes, in my opinion, real intelligence, and all the more so since it was done by wasps in orphan as well as in normal nests. When my cat finds the warmest spot in the house in winter and the coolest in summer, we attribute the action to a thermic sense. If my *pallipes* wasps had, when the heat became oppressive, sought shelter or comfort for themselves, we could likewise attribute the movement to a thermic sense. But here in the face of danger to the young, the wasps used one of the two only reasonable means for protecting them from death,—that of sousing them with water. The alternative method would have been to ventilate the nest by beating of the wings, as I have observed in *P. rubigenosis* some years ago;³ but movement of the air alone would have availed little in this desert heat—in fact, it might have increased desiccation.

This behavior was not due to the idiosyncracies of these individuals, for careful observation sometime later when the weather had returned to normal showed that they resumed their usual program of building and food-gathering.

Another reaction to extreme heat was displayed by these creatures in my yard on August 12. This, you see, was later in the season, when most of the young had arrived at maturity, and needed little attention. All the wasps on one nest and the majority of those on another had their heads thrust deep into the empty cells. I found them thus, and waited to see what this unusual performance might mean. But their patience exceeded mine, and after 35 minutes I grew tired of gazing intently at so inane a piece of behavior, so I left them in the same position. Whether these cells had previously been moistened with water, I do not know. I surmise that they were seeking refuge from the heat, which was intense that afternoon. If I am correct in that assumption, it is interesting to see that they spared themselves no exertion in the extreme heat when the young needed their care, while now, without dependents, they sought comfort for themselves and had abandoned the nest sprinkling habit.

The effect of the drought on the size of the nests and the date of termination of nesting activities was very marked. In the latter part of August, *pallipes* were already abandoning their nests, while in other years this did not occur until about a month later. At a date when nesting activities should still have been in progress, the few young in many nests both in the field and at home, were starved and shrunk. The few adults found on the nests were listless and displayed no inclination to either build up or defend the nest. The nests were about one-third the usual size for this time of year. It is not surprising that this, the worst drought on record in this vicinity,

breast is saturated with water. Therefore it appears that the eggs and the soil on which they are laid are wetted every day, and must tend to prevent overheating." The sand-grouse have also adopted an extraordinary method of watering their young by wetting the feathers and permitting the young to suck the water from them.

³ Paper soon to appear in *Psyche*.

should have wrought this havoc in the wasp population. The vegetation in fields and yards was so dead and dry that grass fires were numerous. Not only were the wasps obliged to perform the additional labor of protecting their young from the abnormal heat, as described above; they also had to face gradually encroaching famine when the drying vegetation deprived them of nectar, pollen and finally of caterpillars. The exception served only to make these conditions more striking: two nests of *P. variatus* built near the edge of a stream, where water and food remained plentiful, were of normal size, and nesting activities continued a month later than in the parched upland regions.

Wheeler has suggested that in time of scarcity of insect food, wasps sometimes provide honey to tide over the emergency. If ever there was a time for emergency provision, this seemed to be one. But in 12 nests examined, only 3 cells contained any honey, and these cells were without young. In this case the theory did not hold. But the reason is not far to seek. In the dried-up vegetation, honey was as scarce as caterpillars.

The adults which were yet to be found on the nests during August were idle. Occasionally one would fly away, and when it returned the others would gather around it, apparently to get some food from its mouth.⁴ In one instance I saw 5 individuals crowding around and climbing over one, until eventually each had had an opportunity to share in the bounty. This is probably a bit of behavior belonging to time of famine, for it appears in *rubigenosis* much later in the year, when they are preparing for hibernation, and famine prevails because frost has killed the vegetation.

Thus we see that to the various accomplishments of *Polistes* wasps we must add the intelligent use of water, in remarkable adaptations to meet the vagaries of environment.

SUMMARY

The welfare of *Polistes* wasps is dependent in large measure upon the available water supply. They carry large quantities of it to drink, to give to the larvae and to use in nest building.

During the intense heat of the drought of 1930, when desert conditions prevailed, the adult *Polistes pallipes* ceased all other work and diligently carried water, drenching the nests to cool the larvae and prevent desiccation. Under identical conditions a little later in the season, when no larvae were in the cells, the adults rested and sought their own comfort. The dry heat and the dearth of vegetation and caterpillars brought the breeding season to an end a month earlier than usual, and greatly reduced the population.

⁴This same process was observed in *P. rubigenosis* later in the season and is described in Entomological News 40: 7-13, 1929.

STUDY OF A PEAT BOG NEAR THE MATAMEK RIVER, QUEBEC, CANADA, BY THE METHOD OF POLLEN ANALYSIS

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PURPOSE

It is the purpose of this paper to trace the history of the vegetation of a bog located in the Province of Quebec, Canada, on the "North Shore," about 15 miles northeast of the mouth of the Moisie River by the method of pollen analysis.

HISTORIC BACKGROUND

According to Erdtman ('27) the idea of gathering information from the study of fossil pollen originated with G. Lagerheim, at the University of Stockholm, during the first decade of this century. The working methods were developed by L. von Post, at the Geological Survey of Sweden, and are described by Erdtman ('21) in another paper.

Extensive studies have been made of the bogs of northern Europe by this method, and much has been learned about the history of the forests and their migration after the recession of the ice sheet.

Little work of this kind has been done thus far in America. Auer ('27) made a study of a series of bogs in southeastern Canada. Lewis and Cocke ('29) worked on peat from the Dismal Swamp of Virginia and North Carolina. Draper ('29) and Sears ('30b) studied some Ohio bogs. Interest in this field is increasing rapidly, and we expect to see many papers on pollen analysis published in the next few years.

CLIMATE AND VEGETATION

The growing season in the Matamek River district is very short. In 1927 the alders, *Alnus crispa*,¹ shed their pollen about the 20th of June, and the conifers, mostly *Pinus Banksiana*, *Picea mariana*, *P. canadensis* and *Abies balsamea*, shed theirs about the 4th of July. It is reported that the first freeze usually occurs during the first week in September. The rocks and soil exposed to the sun in midsummer become hot, but the water of the Gulf of St. Lawrence, and of the streams emptying into it, is very cold. Marie-Victorin ('27, p. 84) says that ice sometimes persists throughout the year

¹ Botanical names, unless otherwise indicated, are those of the seventh edition of Gray's Manual.

deep in soil which is shaded by dense spruce (*Picea* spp.) forests, and we believe this to have been the reason for our inability to penetrate to the bottom of this peat deposit at several points.

The principal forest trees of this district are the spruces, *Picea canadensis* and *P. mariana*, mixed with some fir, *Abies balsamea*, and an occasional large birch, *Betula alba*. Willows, *Salix* spp., and birches are common along the banks of streams. *Pinus Banksiana* was seen in open formation on a dry sandy plain. Alder is common in open moist places. For a more detailed study of the flora of the "North Shore" see St. John ('22), and for further observations on that of the Matamek River district see Bowman (awaiting publication).

AGE OF BOG AND PRESENT COVER

Coleman ('13) estimates that about 25,000 years have elapsed since the spot on which the city of Montreal now stands was uncovered by the receding ice sheet. The Matamek River district is about 500 miles northeast of Montreal, and probably did not emerge until some time later.

According to Hind (1864), the old shoreline which was uncovered by the last glacier has since risen about 1,000 feet and is now some miles inland. This bog rests upon a floor of fine gray sand and clay which is approximately 100 feet above the present sea level.

Since this elevation is about one-tenth of the total rise which appears to have taken place in the last 25,000 years or less, we may estimate the greatest possible age of this bog to be under 2,500 years. The presence of terraces suggests that the land did not rise at a constant rate during this time.

The bog is now covered with an old forest of spruce and fir, under which scattered patches of *Sphagnum* may be found. It is interesting to compare the findings in this bog with those obtained by Auer ('27) in bogs farther south, as this bog is above the northern limits of many of the plants found in the flora of the ones he studied, and is probably much younger.

METHODS

Cores were collected with a Davis peat sampler (Bastin and Davis, '09). This consists essentially of a brass tube containing a pointed plunger (Fig. 1),

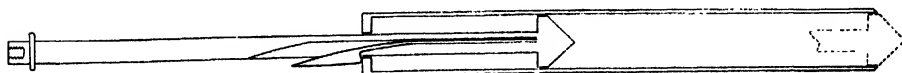


FIG. 1. Davis peat sampler; median longitudinal section.

and brings up a cylinder of peat about $\frac{3}{4}$ inch in diameter and 6 inches long from any desired depth up to the length of the instrument. The handle by

means of which it was pushed down and withdrawn is made of "eighth-inch" iron pipe, which is about $\frac{3}{8}$ inch in outside diameter. This is cut into 2-foot lengths, which are easy to carry and which provide a convenient means of measuring depth, and is surmounted by a cross-piece by means of which to grasp it. In operation the sampler is pushed down to the depth from which it is desired to take a core, and the handle is drawn up gently until the plunger head reaches the top of the tube where it is held by a spring catch. The sampler is then pushed down 6 inches farther, the sharp edges of the tube cutting out a core of peat which fills it. The whole is withdrawn and the spring catch pressed into its slot to release the plunger head which is used as a piston to eject the sample upon a piece of paper.

The cores were rolled up in sheets of newspaper, which is rather absorbent, and labeled as to depth, for example, 5 to 5.5 feet, and as to orientation, that is, which end had been uppermost. We found that labels written on the wrapper with soft black pencil were quite satisfactory, since, although they were obscured by wetting, they became clearly visible again when the paper dried out. It is desirable to spread the rolls in a well-aired place until they are quite dry in order to prevent the growth of molds.

In order to prevent mixing of samples from different depths, successive ones were not taken from the same hole.

To prepare the peat for study, the end of a cylinder was carefully scraped in order to remove any foreign matter which may have adhered to the surface. The upper end was used because the depth of that portion was known. The peat at the lower end of the cylinder may have come from a point 6 or more inches below that at the upper end, according to its compactness and the extent to which it had been compressed in the tube. About a cubic centimeter was cut off, broken up in a beaker, covered with about 25 c.c. of 10 per cent solution of potassium hydroxide, and boiled for 3 to 5 minutes in order thoroughly to separate the particles of which it was composed. This mixture was strained through cheesecloth to remove the larger objects, and then centrifuged to separate the peat from the liquid. The sediment was washed with water to remove most of the potassium hydroxide solution, and then shaken up in 10 c.c. of water to which was added 5 drops of 1 per cent aqueous solution of gentian violet. It was allowed to stain in this for about 10 minutes. The violet not only makes the spores rather easy to see, but colors some elements in the peat differently, for instance, birch spores usually appear red and certain egg cases (?) blue. The stained material was then passed quickly through 95 per cent alcohol, absolute alcohol (100 per cent), and xylol, after which it was stirred up in several drops of Canada balsam and distributed over about 10 slides, to which were applied 22×40 mm. cover slips.

We have since found that very satisfactory results may be obtained by staining with an aqueous solution of safranin which is added to the potassium

hydroxide solution in which the peat is boiled. This eliminates one step in the process of preparation, and gives a more uniform stain than the violet.

These samples were then studied with the aid of a mechanical stage. After each trip across the slide horizontally the stage was advanced 1 m.m., which left an unobserved area between each pair of bands in which the spores were counted, and thus avoided counting the same ones twice, because the diameter of the field was less than 1 m.m. For these observations a 4 mm., objective and 15-x oculars were used. At the start of each transit of the slide the reading of the vertical scale of the mechanical stage was recorded, with an arrow by its side to indicate the apparent direction in which objects in the field were to be moved. Such a device permits one to continue after interruptions without danger of duplicate counting.

We now use an 8 m.m. objective. Because of its greater working distance this lens is less likely to come in contact with the cover glass, which happens with the 4 m.m. objective when the sample on the slide is a bit thick. Its larger field permits one to count more spores in a single transit of the slide. The greater depth of focus makes the field easier to look at, and reduces eye strain.

A camera-lucida was kept in position while observations were being made, so that as objects of interest were found they could be drawn accurately for future study, and so that the image of an unknown specimen could be superimposed upon a drawing of a known one and directly compared with it.

Identification of unknown pollens is based for the most part on comparisons with material the identity of which is known. Slides are made of fresh pollen during the summer as plants are collected. When fresh material is not available, pollen is obtained by boiling anthers from dried specimens. A number of collections of each kind should be made from different sources and compared in order to avoid errors in identification, as the spores of *Betula* are sometimes formed with 4 pores instead of 3, and capsules of *Sphagnum*, instead of containing the usual angular spores, may be filled with the spherical ones of *Tilletia sphagni* (Nawaschin, 1890).

Some of the first papers published on the identification of pollen dealt with the subject from the standpoint of the bee-keeper (Betts, '25 and Young, '08). The study of pollens as a cause of hay-fever has brought out more literature. In these fields the interest lies in fresh material, and the nature of the stored food as well as the date of shedding are used as aids in identification (Scheppegrell, '22, and Moore and LaGarde, '26). In the study of fossil pollens one must depend entirely upon the characteristics of the wall, such as size, shape, number of pores and grooves, and nature of the sculpturing if any. The drawings published by Meinke ('27) are rather helpful, as are also those of Lewis and Cocke ('29) and Sears ('30a). The classic work of von Mohl (1835), although it deals with few of the genera usually found in peat, is of considerable interest in that it indicates clearly the different appearances which may be presented by the same pollen-grain

according to the angle from which it is viewed, or whether it be shrunken or expanded. Pope ('25) and Wodehouse ('26 and '28) have written on pollen morphology as an index to plant relationship.

The point to which the identification of a pollen-grain can be carried varies greatly according to its family. The pollens of grasses (Gramineae) and sedges (Cyperaceae) are recognizable as such, but we are not yet able clearly to identify genera. Those of fir, spruce and pine can usually be separated on the basis of size, but some overlapping of the size ranges occurs, and they must then be distinguished by differences in form. Chemical treatment may bring out variations in structure not otherwise evident (Jentys-Szafer, '28). The spores of various species of *Lycopodium* differ considerably. A thorough and systematic treatment of different groups of spores which would include information as to the variation in size and form, and a good picture of an average spore of each species, would be a great help to those engaged in pollen analysis.

There are different opinions on the question of how many spores to count in order to obtain reliable figures on the relative density of the different kinds present. Lewis and Cocke ('29, p. 40) say: "In counting the different pollens for reckoning the percentage of any given species, 800 grains were counted from each depth." Sears ('30b, p. 210) says: "At least 2 slides were prepared from each sample. . . . Wherever possible, at least 100 grains were counted from each slide." Erdtman ('31, p. 400) says: "Trustworthy percentages are obtained if about 150 pollen-grains are counted." The results shown in this paper are based on counts of 1,000 to 1,800. The problem of interpretation of results is further complicated by the fact that some authors include in their count the spores of Bryophytes and Pteridophytes, whereas others include only "forest trees." Until some uniform procedure which will make published results comparable is agreed upon it is strongly recommended that a clear statement as to how the percentages were calculated be included in each paper.

The following observations were made to indicate the degree of error which may be expected from counts of various numbers of spores. In Table

TABLE I. *Number of each kind of spore found per hundred for twenty different hundreds, all from one sample on one slide*

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	Av.*	Total
Betula.....	20	31	25	18	19	25	19	31	28	26	20	33	19	21	26	25	24	27	31	28	25.1	505
Sphagnum.....	16	18	20	28	27	24	22	19	15	21	26	15	23	20	25	21	22	19	20	27	21.4	428
Sedge.....	18	18	14	22	17	17	21	20	16	21	20	17	12	20	23	20	19	20	22	19	18.8	376
Picea.....	8	9	12	16	21	7	13	11	16	14	16	12	20	13	11	8	14	13	12	10	12.8	256
Alnus.....	10	16	14	5	4	7	5	9	7	4	5	3	6	10	7	5	2	5	3	3	6.5	130
Abies.....	5	2	2	1	4	7	11	3	7	8	5	12	6	3	4	10	9	7	6	3	5.8	115
Pinus.....	1	3	3	4	3	5	2	3	1	2	0	5	2	2	2	0	0	6	3	2	2.5	50
Ericaceae.....	1	0	2	2	0	1	1	1	3	0	1	2	1	1	0	1	0	0	0	2	1.0	19
Ferns.....	3	1	1	0	0	3	0	2	0	0	1	1	1	1	0	1	1	0	0	0	0.8	16
Lycopodium.....	0	0	0	1	2	0	0	0	0	2	0	0	0	1	1	1	1	0	0	1	0.5	10
Others.....	9	2	7	4	2	6	3	2	3	5	4	5	6	8	1	8	9	3	3	5		

* Average based on total count of two thousand.

It is shown the percentage of each kind of spore identified in 20 different counts of 100 each, taken from a single slide, and recorded in the order in which they were made. The sample was thoroughly mixed and spread before the cover glass was applied. Note especially the fourth, sixth and twelfth hundreds. Fig. 2 shows graphically the averages obtained from the

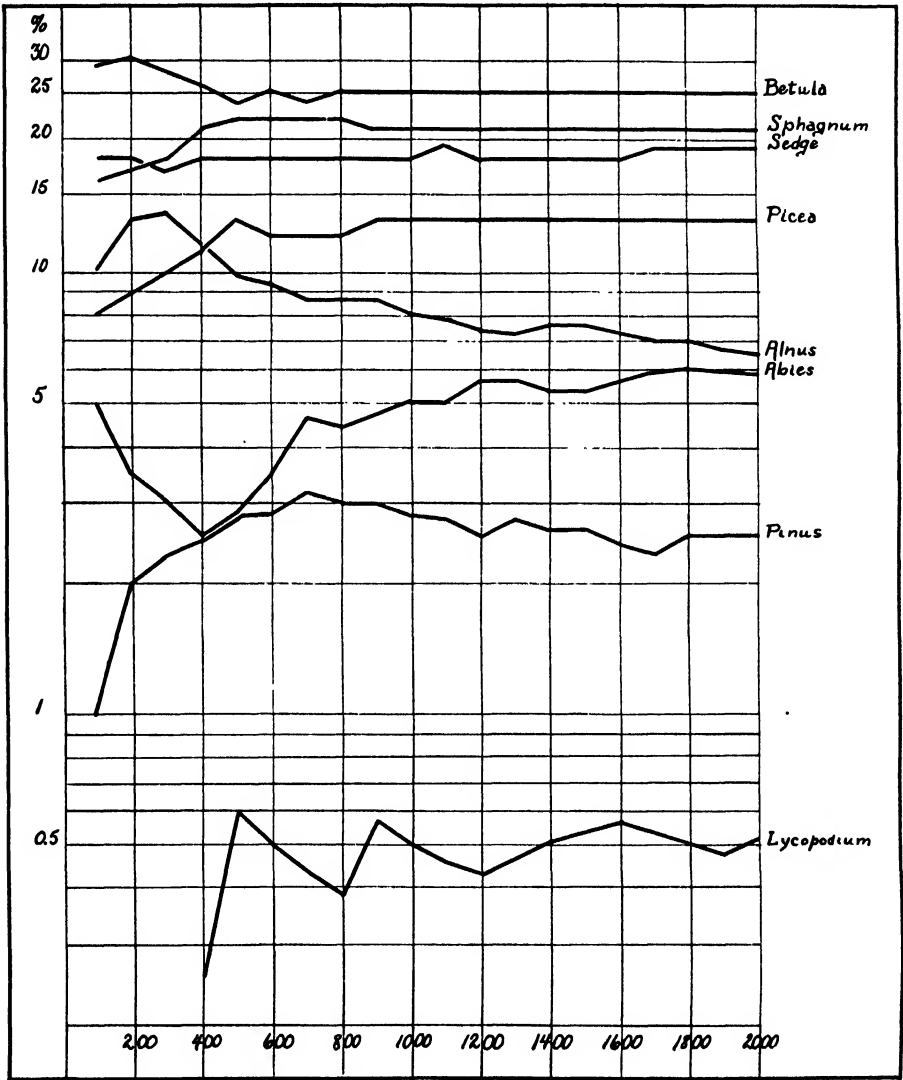


FIG. 2. Curves showing how the percentages of various kinds of spores counted in one sample on one slide vary as the number of spores counted is increased.

first hundred, the first two hundred, the first three hundred, and so on, the last values representing the averages obtained from the entire twenty hun-

dred. The percentages are drawn on a logarithmic scale so that the variations shown are comparable in degree.

Marked differences have been noted in the concentration of spores, that is, the total number per cubic centimeter of peat, at different levels (Auer, '27). Malmström ('23, pp. 198-199) observes that the concentration is greatest in sedge peat (Cyperaceantorf). Our findings are in accord with this statement. Not only is the concentration in the lower half of the deposit, where sedge is found, greater than in the upper half, but in general the points of greatest concentration coincide with maxima in the sedge curve. The figures showing relative concentration are presented in Table II. It seems that a certain amount of concentration is to be expected in the lower levels, because disintegrating influences have had longer to operate on that material and because it is compressed by the weight of the peat above it.

The record of different kinds of spores observed, and the percentage of each at each level, is given in condensed form in Table II. Interpretation of such records is usually based on the assumption that windblown pollens are uniformly distributed, which appears to be true for small areas. When one tries to form a picture of the flora as it existed at some time in the past from a count of fossil pollen-grains it must be kept in mind that a certain group of spores may have come from a few plants nearby or from many plants at a distance, and also that some pollen-grains are more delicate than others and seem not to be preserved in peat, for instance, *Chamaccyparis* and *Taxodium* (Lewis, '29, p. 41), *Juniperus* and *Thuja* (Scars, '30a, p. 101), and *Populus* (Erdtman, '31, p. 401). In spite of these limitations, the evidence of pollen-analysis is valuable in interpreting plant history, for the presence of certain forms and the changes which took place in the relative quantities of these can be definitely established.

ANALYSIS

The problem is from the counts at all levels to construct frequency curves for all kinds of pollen found, and to interpret these in terms of dominance and succession. It is desired also from such studies to draw conclusions as to the nature of climatic changes which have taken place in the past, but this cannot be done until a great many observations shall have been made over a large area, so that nonsignificant variations due to local conditions may be eliminated.

The frequency curves (see Figs. 3 to 6), which are based on per cent of total spores exclusive of fungi, show how various elements in the flora of this bog rose to a position of dominance and then declined. These will now be discussed in detail.

Let us consider first the curve of spruce, *Picea spp.* (Fig. 3), as it is one of the elements of major importance. Its general trend is upward to its present position of dominance, but its advance is by a series of oscillations in the course of which it presents 6 maxima.

TABLE II. *Percentage of various spores at each level*

Depth in ft.	<i>Picea</i>	<i>Betula</i>	<i>Pinus</i>	<i>Abies</i>	<i>Alnus</i>	<i>Erica- ceae</i>	<i>Lycopodium</i>	Ferns	<i>Sphagnum</i>	<i>Salix</i>	<i>Compositae</i>	Sedge	<i>Aster</i>	<i>Tsuga</i>	Gram- ineae	Fungi			Dia- tomis	Un- knowns	*Den- sity of spores counted
																A	B	C			
0	42.6%	13.7%	7.7%	14.3%	1.3%	2.8%	0.7%	0.2%	5.3%	0.2%	0.9%	0.7%	0.1%		4.5%	0.3%	0.3%		0.5%	4.6%	600
1	53.6	5.7	5.7	15.3	0.3	2.2	0.8		13.6		0.1		0.1			0.1			0.1	2.7	410
2	36.5	4.8	2.7	9.5		0.3	0.4	0.5	39.6							3.6			0.4	2.0	260
3	23.6	30.0	5.0	3.6	1.2	3.0	0.4	0.2	25.2	0.1						1.9	5.0		0.4	5.1	590
4	8.1	6.4	1.0	1.1	0.1	0.1	0.1	0.1	80.3				0.1		0.2	1.2	1.0		0.4	1.4	1250
5	25.7	6.2	2.4	4.2	0.5	0.8	0.1	0.2	55.9							1.8	2.2	0.1%	0.3	1.7	1475
6	38.5	13.7	2.9	7.5	0.3	1.0	0.1	0.3	31.9	1.6						36.0			0.1	1.3	1300
7	26.9	13.8	1.5	4.7	0.5	4.3	0.7	0.3	43.9	0.3	0.1					0.9	2.9		0.3	1.7	1364
8	20.8	14.3	1.7	3.0	0.5	2.7	0.1	0.1	54.9		0.1				0.1	0.9	0.7		0.3	0.9	1620
9	32.8	5.9	2.8	4.4	0.2	1.6	0.2	0.1	48.2	0.2						0.8	1.2		0.3	1.6	1880
10	16.9	25.1	0.8	2.6	0.4	1.6	0.7	0.2	36.3	0.6	0.1	9.1	0.1	0.2%	0.1	2.1	2.6		0.2	2.5	9400
11	12.2	12.0	0.4	3.0	0.4	0.2	0.5	0.4	59.6	0.2	0.2	3.9	0.3	0.2		1.4	20.2		0.3	4.8	2880
12	20.3	21.0	2.0	1.7	0.7	0.9	0.9	0.5	37.1	0.2	0.1	10.1	0.8	0.1		2.1	1.7		0.5	1.3	6320
13	16.0	21.3	2.2	3.0	0.6	0.1	3.3	0.8	3.7	0.2	0.2	9.3	1.8	0.3		0.1	5.1	0.1	0.5	3.0	770
14	19.9	22.3	2.4	5.9	1.2	0.7	1.5	0.4	33.7	0.5	0.1	8.4	0.1			1.4	10.0	0.2	0.2	1.7	2540
15	15.5	15.3	1.9	14.7	5.6	0.6	0.4	0.5	42.5	0.2	0.1	3.5	0.2	0.1		1.7	5.5	0.3	0.1	3.0	3710
16	12.2	29.1	1.1	9.3	4.4	0.2	1.0	0.8	24.2	0.1		12.0	0.7	0.1		0.3	0.5	1.8	3.0	1.8	1980
17	27.3	15.3	2.1	33.0	5.2	0.7	1.2	0.7	4.6	0.5	0.2	7.5	0.3			0.3	0.5	0.3	0.3	3.9	950
18	9.9	24.2	2.2	5.2	4.4	0.4	1.6	0.1	28.3		0.2	16.4				1.3	4.9	0.5	0.3	3.9	1540
19	14.4	24.2	1.9	4.3	8.7	0.6	0.1	0.5	23.7	0.1	0.1	16.4				1.2	6.7	0.8	0.8	3.1	2000
20	15.5	24.2	1.5	4.6	4.1	0.5	1.1	0.5	30.8	0.1	0.4	10.1	0.3			1.2	11.4	0.4	0.4	5.2	1430
21	14.9	25.5	1.2	5.5	5.4	1.4	1.0	0.9	28.3	0.2	0.2	9.4	0.3	0.2		2.5	6.9	0.2	0.2	3.0	3330
22	7.1	10.0	0.9	3.6	1.4	0.1	0.1	0.3	1.6	0.1	0.1	71.9	0.2			0.2	0.3	0.1	0.4	2.2	5000

† These percentages are based on the total of all spores listed except fungi.

* * Relative density of spores in different samples is indicated by the approximate number counted in twenty transits of a slide.

The curve of birch, *Betula*, shows a general downward tendency upon which has been imposed the same set of secondary fluctuations.

Further study of these curves shows that they cross at about the 5½ foot level, below which birch was most abundant and above which spruce is dominant.

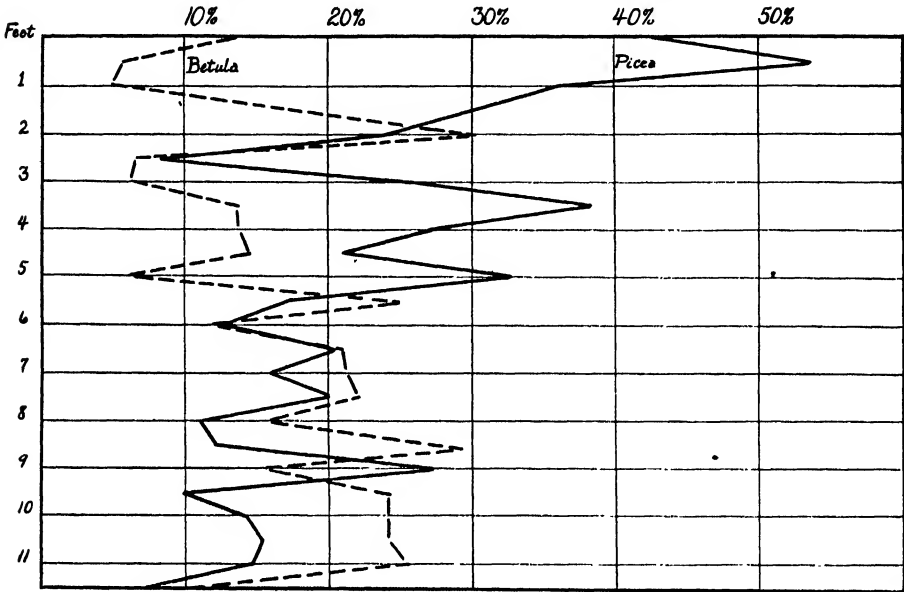


FIG. 3. Curves of *Betula* and *Picea*.

The corresponding maxima and minima of the spruce and birch curves do not always occur at the same depth. Below 5½ feet spruce seems to respond more quickly to the causes of these secondary variations whatever they may have been, than birch. Above this level the reverse is true. For example, a spruce peak occurs at 9 feet and the corresponding birch peak is seen at 8½, whereas the spruce peak at 5 feet has its corresponding birch peak at 5½.

These points focus our attention upon the 5½-foot level which we find to be of peculiar interest because it seems to mark the end of a period during which this area was being invaded by trees, and the beginning of one during which the entire area was covered with trees.

The main point in support of this conclusion is the presence of sedge pollen, Cyperaceae, in decreasing but appreciable quantities up to this level, and its absence beyond, except for an insignificant bit at the surface (see Fig. 4). If we consider that a relatively enormous quantity of pollen is shed by any one of the trees found here, especially the conifers, Pinaceae, as compared to that shed by a stand of sedge covering the same area, and that sedge does not ordinarily grow in the forest under trees, but rather out in

the light, the picture representing this stage of development must be one of a great open swamp over which are scattered small groups of trees, growing probably on the higher and dryer spots.

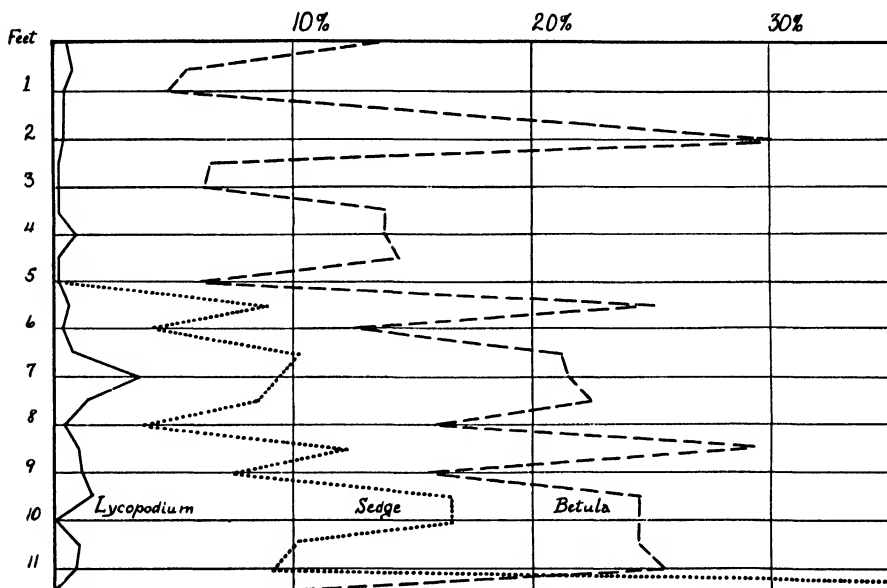


FIG. 4. Curves of *Betula*, *Sedge* and *Lycopodium*.

In the upper levels of the peat the spores of certain forms, Compositae, Cyperaceae, *Acer*, *Tsuga*, *Abies*, *Alnus*, *Lycopodium* and Filicales (see Table II and Figs. 4 and 5), are absent or decidedly reduced in quantity. Such a change could have been brought about by increased shade (Nichols, '15, p. 209) and by increased competition and it, also, suggests that the growth over this bog in its later stages of development was a closed forest.

These findings support Auer ('27) in his contention that the flora of the earlier period of the bogs of this region was richer in genera than that which formed the upper layers. This point is most clearly illustrated in Table II, in which is listed the percentage of each kind of spore found at each level.

The origin of this deposit as a sedge swamp growing on a foundation of glacial till, and its later development by increased growth of *Sphagnum* and decline and disappearance of the sedge (see Fig. 5), are in agreement with Auer's statement ('27, p. 14) that in the ocean area, as contrasted with the continental or inland area, peat bogs usually arise on dry land or on land recently exposed by recession of the shoreline, and consist of a thin lower stratum of *Carex* covered with a thick deposit of *Sphagnum* (p. 9).

The *Sphagnum* maximum occurs at 2½ feet and exceeds 80 per cent. There is, generally speaking, a peak in the *Sphagnum* curve corresponding

to each major depression in the spruce curve (see Fig. 5). When an area of *Sphagnum* becomes covered with trees the growth of the *Sphagnum* is greatly reduced because of the shade. If the forest breaks down, however,

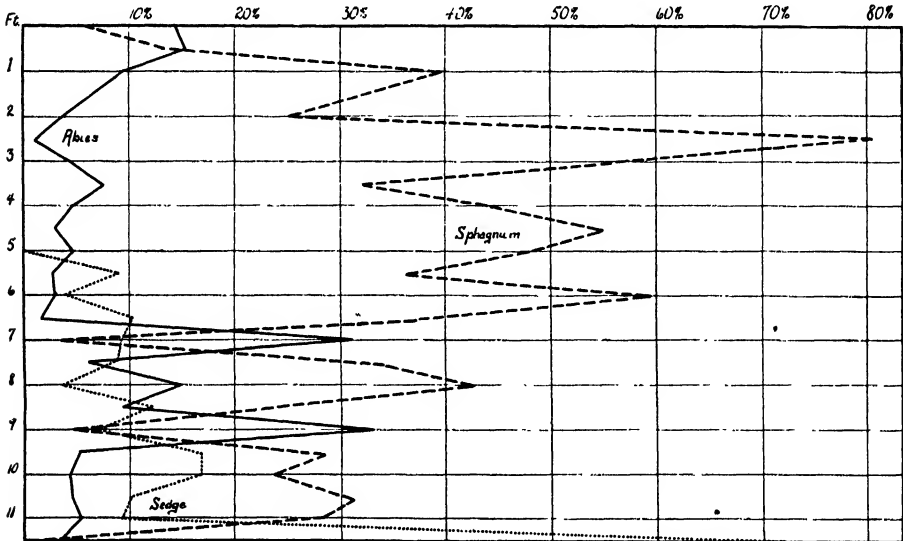


FIG. 5. Curves of Sedge, *Sphagnum* and *Abies*.

before the *Sphagnum* has been entirely killed off the latter will flourish and cover the area once more, sometimes burying the remains of the forest. Buried trees were occasionally struck by the sampler in this deposit.

The curve of fir, *Abies*, (see Fig. 5) in a general way follows that of spruce. It rises sharply to its highest points at the 9- and 7-foot levels, where it exceeds 30 per cent, and is for a short time more abundant than spruce or birch. These peaks, which coincide with spruce maxima and *Sphagnum* minima, suggest that for those two periods there existed temperature, rainfall and soil conditions much more favorable than usual to the dissemination and growth of fir trees.

Pine, *Pinus Banksiana*, was not observed as part of the bog flora, but was seen on sandy, well-drained areas some distance off. Its pollen will carry in the air for great distances, and it is quite possible that the spores found were blown in from the surrounding country.

Traces of grass were found at some of the upper levels, with a maximum of 4.5 per cent at the surface. Grasses are now found in small quantities wherever an open space occurs.

A rise in the Ericaceae seems to accompany the increase in trees which follows each *Sphagnum* peak, the highest occurring at the 4- and 2-foot levels.

The fungi were not included in the spore count because in some cases, especially where spore masses occurred, it was not possible to count them

with any degree of accuracy. Three kinds of fungus spores were found which occurred singly and could easily be recognized, and the count of them is shown in Table II. Spore "A" is spherical and reticulated, and resembles the spores of *Tilletia*. "B" is 2-celled and 4 to 5 times as long as wide. "C" is $1\frac{1}{2}$ to 2 times as long as wide, flat, and curiously lobed. Their percentage was calculated on the same basis as that of the other kinds recorded. At the 2-foot level a great quantity of fungus spores and spore masses was observed, many of them in bits of wood and other debris, which suggests that at that time the destruction of the forest which fell before the *Sphagnum* maximum at $2\frac{1}{2}$ feet was at its height.

A diatom, of the Centricae, was found in small quantities at nearly all levels.

The quantity of unidentified spores is low, due in part to the lack of any great variety and in part to the fact that most of the spores in this peat are easily recognized.

The curve of each plant or group of plants represented in the flora of this bog, so far as we were able to determine them, shows a large general tendency peculiar to itself upon which are imposed a series of secondary oscillations common to all.

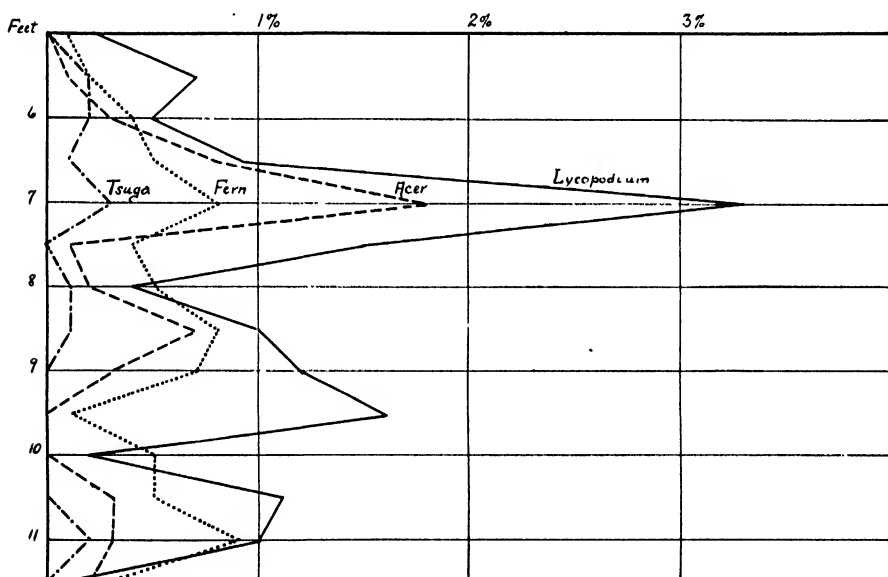


FIG. 6. Curves of *Lycopodium*, *Acer*, *Fern* and *Tsuga* from five-foot level to the bottom of the bog.

Spruce and birch each show 6 maxima (see Fig. 3). The 4 of these which fall between the 11- and 5-foot levels can be matched by a similar set in sedge and *Lycopodium* (see Fig. 4), and in *Acer*, ferns and *Tsuga* (see

Fig. 6). These common secondary oscillations we believe to be reflections of climatic changes, for instance, variations in temperature and rainfall.

Sedge drops from a maximum of over 70 per cent in the lowest layer to extinction at 5 feet. From the bottom to the surface, birch steadily loses ground and spruce gains. *Acer* and *Lycopodium* reach their peaks at 7 feet, Ericaceae at 4, *Sphagnum* at $2\frac{1}{2}$, spruce at $\frac{1}{2}$, and *Pinus*, Compositae and Gramineae (which first appear at $5\frac{1}{2}$ feet) have their maxima at the surface. These large general tendencies we believe to be reflections of edaphic influences, that is, variations in the condition of the soil as to alkalinity or acidity, water content, chemical composition, degree of disintegration, etc. (Bray, '21).

SUMMARY

Cores of peat were taken from a Quebec bog, and samples selected at 6-inch intervals were stained and mounted on slides for study. At least 1,000 spores were counted from each sample, and a record made of the number of each kind present. Curves were drawn to show the relative density of each kind of spore at each level. The curves show this to be an ocean type bog, with sedge present in the lower levels and *Sphagnum* in the upper. The curves also suggest that the bog went through an open marsh stage to one of closed forest. Each curve shows an individual trend and a set of secondary oscillations common to nearly all.

ACKNOWLEDGMENTS

In the spring of 1927 Mr. Copley Amory, of Washington, acting upon the recommendation of Dr. Paul Bartsch, of the National Museum, invited us to spend the summer on his estate on the Matamek River to study the flora of that district, which is little visited and which he believed held much of interest to the naturalist. Mr. Amory very kindly provided transportation for us and our equipment from Quebec; and, to further our work during the summer, he not only put the facilities of his place at our disposal, but personally took us on excursions to places which we would otherwise not have visited.

The study of fossil pollen in peat was first brought to our attention by Dr. Ivey F. Lewis, of the University of Virginia, whose aid in solving many of the problems which arose during this work we gratefully acknowledge. We also wish to thank Dr. A. P. Dachnowski-Stokes for his directions as to the construction and use of the peat sampler, Mrs. P. W. Bowman for her assistance in the collection of the samples, Dr. R. A. Quick for the use of the centrifuge with which the material was prepared for study, Dr. J. M. Fogg, Jr., for aid in the collection and identification of plants for the study of pollens, Mr. W. W. Diehl for suggestions and assistance in the study of fungus spores, Dr. O. C. Durham for pollen samples, and our other friends who have assisted in ways too varied and numerous to mention.

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STUDIES IN NOCTURNAL ECOLOGY WITH SPECIAL REFERENCE TO CLIMAX FOREST¹

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INTRODUCTION

A large body of data has been gathered upon the activity of nocturnal animals, and upon the inactivity of diurnal animals at night, both for solitary individuals and sleeping aggregations. This is especially true for mammals (Bachman, 1837; Shull, '07; Seton, '09; Warren, '10; Johnson, '26; Sherman, '29; Gregory, '30) and for birds (Brewster, 1890; Bates, 1895; Jones, 1897; Montgomery, 1899; Hunt, '06; Townsend, '18; Widman, '22). Sleeping attitudes and nocturnal activity have been observed in fish (Werner, '11; Cahn, '27, pp. 62-91; Rounsefell, '29, p. 231) and in other vertebrates mentioned later. Many invertebrates are known to be active at night, *e.g.* crayfish (Newcombe, '29, p. 275) and earthworms (Baldwin, '17) in addition to insects which will be discussed in some detail. Similarly, the nocturnal activity of many marine species has been described by Polimanti ('11).

It becomes clear from this literature that there is a characteristic nocturnal, as well as a diurnal fauna. These papers dealing with nocturnal species are valuable for purposes of comparative autecology, but, due to a lack of adequate measurement of environmental factors or of community intra-action in most cases, such accounts have not tended to advance our knowledge of the ecological community at night, *per se*.

One of the few attacks on the general problem was made by Chapman and his colleagues ('26) in a study of the insects of a Minnesota sand dune. There is a great deal to learn about the movements and interactions of nocturnal animals throughout the night, and nocturnal ecology has been pointed out as a practically untouched field of research (Allee, '27). The present report is a preliminary attempt to further our knowledge concerning nocturnal ecology, especially of the beech-maple forest.

AREA AND METHOD OF STUDY

The observations reported here were made on two 80 acre tracts of comparatively primary beech-maple forest in northeastern Ohio,² Allyn's

¹ Contribution from the Zoölogical Laboratories of the University of Illinois No. 407.

² A summary of these data has been reported (*Bull. Ecol. Soc.*, 11(4) : 8, 1930). We are indebted to Mr. J. A. Allyn and Mrs. H. H. Haas for permission to use their

Woods, located near Hiram, Ohio, and Haas Forest, near Twin Lakes, Ohio. As far as could be observed, both forests were in a state of good preservation. In the former, rough roads traversed the tract, and many maples had been tapped for their sap. Beyond this, and the inevitable cutting of most of the adjacent timber, little biotic disturbance was apparent. In both forests, the floor was covered with mesophytic herbs, ferns, and mosses. Woody fungi, e.g. *Fomes*, were abundant, and there was a profusion of decaying stumps and logs. The following list of plants serves to characterize the communities studied.

TABLE I. *Typical plants from Allyn's Woods, Hiram, Ohio*

Tree stratum	Shrub stratum	Herbaceous stratum
* <i>Fagus grandifolia</i> Ehrh.	* <i>Pseodera quinque-</i>	* <i>Eupatorium urticaefolium</i> Reich.
* <i>Acer saccharum</i> Marsh.	folia Gr.	* <i>Asarum canadense</i> L.
* <i>Prunus serotina</i> Ehrh.	<i>Vitis vulpina</i> L.	<i>Sanguinaria canadensis</i> L.
<i>Quercus rubra</i> L.	* <i>Sambucus racemosa</i>	* <i>Trillium grandiflorum</i> Salisb.
<i>Quercus alba</i> L.	L.	* <i>Impatiens biflora</i> Walt.
<i>Carya ovata</i> K. Koch.		* <i>Polystichum acrostichoides</i> (Michx.) S.
<i>Carpinus caroliniana</i> Walt.		<i>Botrychium virginianum</i> (L.) Sw.
<i>Ostrya virginiana</i> K. Koch.		<i>Adiantum pedatum</i> L.
		<i>Onoclea sensibilis</i> L.

* Dominant or very abundant species.

As far as could be determined, the factor complex, and the biota of both forests were ecologically equivalent.

The period of observations extended over 4 months, April to July, in which 5 trips of from 1 to 2 nights each were made for purposes of orientation. Following this preliminary survey, 3 trips of from 1 to 3 nights each were made to Allyn's Woods (May 18-25, 1930), and 2 to Haas Forest (July 4-18, 1930).

The method employed in each forest was as follows: To intensify observation, a limited number of stations was established in the forest, generally running in a line from the forest margin towards the center. To render these stations accessible for night work, those towards the center were connected by a trail blazed with white paint, and each station was given a number in white paint. Thirty-one stations were established in Allyn's Woods, and 9 in Haas Forest.

These stations comprised a variety of materials: boards laid on the forest floor; shingles and flaps of bark attached loosely by one end against stumps, logs, and trees; logs and stumps in the several stages of the decay cycle (Shelford, '13, pp. 246-247); grape vines; groups of fungi (*Fomes*, *Polyporus*, *Pezizia*, *Myxomycetes*); dung, and the forest floor, *per se*.

A station for the recording of instrumental data was established at each end of each trail, e.g., one in the more open margin at, or near, the beginning land; to Miss Ethel Gowans, Mr. Park Welton, Jr., Miss Luella Konzett, and Mr. Jack Keller of Kent State College, and to Dr. J. H. Turner, of Hiram College, for favors received during the progress of the work.

of the trail, and one in the forest proper, at the end of the trail. Neither the Allyn nor the Haas trail was more than 200 meters in length. Each instrumental station was equipped with a soil-point thermometer, a metal-cased air thermometer, and a sling psychrometer, all from the Taylor Instrument Company, and a Livingston atmometer bulb attached to a burette graduated to two-tenths of a c.c. Data were also obtained with a recording evaporimeter.³

The data were obtained as follows: Temperature of air and of soil at varying depths, relative humidity, rate of evaporation, and wind direction were recorded at the marginal station (Station A). Following these observations, each forest trail station was visited in order, and at the last of these the physical factors listed above were measured at the interior instrumental station (Station B). The return on the trail was now made as rapidly as possible, and a third set of instrumental readings were taken at the beginning of the trail (Station A).

Running of the trail occupied from 30 to 50 minutes of the hour as a rule, and the trail was visited every hour, or in some cases every 2 hours, throughout the night. Usually the recording of observations began at 4:00 P.M. on Saturday and extended into Sunday afternoon or night. Each forest station was visited at about the same time interval on each run along the trail, the ecological observations being made with the aid of flash-lights and gasoline lantern. In all cases, illumination of the stations was avoided as much as possible at night.

If a station was found to be unproductive it was abandoned, and others were established. Only the relatively abundant and characteristic animals were observed, belonging to well known and accurately determined species. The Coleoptera, gasteropods, and salamanders studied were not found to be active by day. All of these species frequently have been observed inactive in their habitat niches during the day by the senior author.

In a number of instances, an animal which was in all probability the same individual was observed in a particular niche on different occasions. In such cases, these individuals were not marked. Marking would yield more positive information if successful, but the probability of destroying the rhythm of the active individual outweighed the obvious advantages in this preliminary survey. Observations upon the activity of marked individuals is a logical continuation of this preliminary study, and is being undertaken at the present time.

PRESENTATION OF DATA

1. *The Species Studied*

Table II presents the species upon which this report is based, and the number of times individuals of each species were observed.

³ Description of apparatus to be published separately.

TABLE II. *List of species, and number of times individuals of each were observed*

Species	Number of times individuals were observed. Adult unless otherwise noted
Coleoptera	
1. <i>Agathidium oniscoides</i> Beauv.	1
2. <i>Boletotherus cornutus</i> (Panz.)	175
3. <i>Chlaenius nemoralis</i> Say.	4
4. <i>Cicindela sexguttata</i> Fab.	3
5. <i>Conosoma crassum</i> Grav.	36
6. <i>Dendroides bicolor</i> Newm.	4
7. <i>Galerita janus</i> Fab.	13
8. <i>Harpalus pennsylvanicus</i> DeG. (?)	1
9. <i>Leiodes blanchardi</i> Lec.	81
10. <i>Megalodacne heros</i> (Say)	5
11. <i>Melanodrya striata</i> Say.	20
12. <i>Meracantha contracta</i> (Beauv.)	6
13. <i>Ontholestes cingulatus</i> (Grav.)	12
14. <i>Penthe pimelia</i> (Fab.)	1
15. <i>Phenolia grossa</i> (Fab.)	8
16. <i>Philonthus cyanipennis</i> (Fab.)	1
17. <i>Platynus hypolithos</i> (Say)	27
18. <i>Pterostichini</i> (spp.)	22
19. <i>Staphylinus violaceus</i> Grav.	1
Hymenoptera	
20. <i>Aphaenogaster fulva</i> Roger.	18*
Diplopoda	
21. <i>Polydesmus serratus</i> Say.	29
Gasteropoda	
22. <i>Anguispira alternata</i> (Say)	199
23. <i>Philomycus carolinensis</i> Bosc.	286
Amphibia	
24. <i>Plethodon cinereus</i> (Green)	3
25. <i>Rana sylvatica</i> LeC.	5
26. <i>Triturus viridescens</i> Raf.	18†

* Eighteen observations, but many individuals seen each time.

† Second larval stage (terrestrial).

2. Period of Activity

The data collected indicate that the nocturnal species observed have a definite day-night rhythm, although it is probable that hunger or other physiological states, and adverse environmental conditions, may alter or destroy such a cycle of behavior temporarily. Thus it would appear that certain species are apparently active at more or less definite periods in the night, and are correspondingly inactive, or apparently so, during the day.

In this report, all readings are based on Eastern Standard Time. Secondly, to avoid error in interpretation, the term "activity" has been restricted to those individuals which were in motion, and which were not occupying their respective shelter niches when recorded. No attempt was made to count inactive animals in general, due to the danger of overlooking many resting forms. However, data were compiled on a number of species where it was probable that a certain individual frequented a particular habitat niche. In such instances both active and inactive periods could be accurately observed. These cases are dealt with later.

Although data were collected on gasteropods, myriopods, amphibians and insects (Table II), the behavior of nocturnal Coleoptera has been emphasized. This is due to the number of beetles found to be active at night, and to the senior author's familiarity with the group as ecological material. In Table III, some of the species are treated which were found to be typically nocturnal, viz. those forms which were active all or a part of the night, and inactive during the day.

TABLE III. *Range of activity*

Species	First observed individual	Last observed individual
<i>Agathidium oniscoides</i> Beauv.....	8:43 P.M.	
<i>Boletotherus cornutus</i> (Panz.).....	7:02 P.M.	6:27 A.M.
<i>Chlaenius nemoralis</i> Say.....	8:46 P.M.	
<i>Dendroides bicolor</i> New.....	9:46 P.M.	11:40 P.M.
<i>Galerita janus</i> Fab.....	8:30 P.M.	
<i>Harpalus pennsylvanicus</i> DeG.?.....	8:59 P.M.	
<i>Leiodes blanchardi</i> Lec.....	7:13 P.M.	8:55 A.M.
<i>Megalodacne heros</i> (Say).....	9:18 P.M.	3:30 A.M.
<i>Meracantha contracta</i> (Beauv.).....	11:23 P.M.	1:19 A.M.
<i>Ontholestes cingulatus</i> (Grav.).....	7:28 P.M.	
<i>Phenolia grossa</i> (Fab.).....	9:37 P.M.	8:35 A.M.
<i>Philonthus cyanipennis</i> (Fab.).....	5:33 P.M.	
<i>Platynus hypolithos</i> (Say).....	8:35 P.M.	1:30 A.M.
<i>Conosoma crassum</i> Grav.....	6:35 P.M.	7:30 A.M.

From Table III it will be seen that the average range of activity of 14 nocturnal species of beetles roughly covers the duration of the night (8:23 P.M. to 4:41 A.M.). When the peculiarities of night observation are realized, the departure of the averages from the extremes, as given in the table (6:35 P.M. to 8:55 A.M.), is not unusually great. Concerning the last observed individual of a species, a number of species held individuals which were known to inhabit certain niches, and here the danger of destroying the niches by handling prevented us in some cases from obtaining data on the end of their period of activity. In other cases, random wandering of animals was made the basis for interpreting the period of activity. Under such conditions, the standard deviation for the first observed individual (1 hour and 26 minutes), and that of the last observed individual (3 hours and 23 minutes) are not too large.

When the behavior of a single species was examined, it was found that there were more individuals active towards the middle of the night than in early evening or near dawn. This conclusion is based upon the species studied, and does not imply that other animals have their maximum activity only at this period. In fact, some records indicate that species may have more than one maximum activity period; and it is highly probable that the factor complex regulates and modifies the nocturnal reactions of animals, as will be seen later. That nocturnal species tend to have regular, definite periods of activity has been pointed out in the case of earthworms by Baldwin ('17). Other species tend to be active through the night for longer periods of time, e.g., forest deer mice (Johnson, '26).

In figure 1, the nocturnal activity of two species is given for a single night. The data presented on activity are in terms of percentage of active individuals observed at different times through the night. In each case the maximum appearance of individuals at one time is taken as 100 per cent. These two species are taken as typical nocturnal forms, similar data being collected for the other species studied. In figure 1 it will be seen that the greatest activity is after sundown and before sunrise.

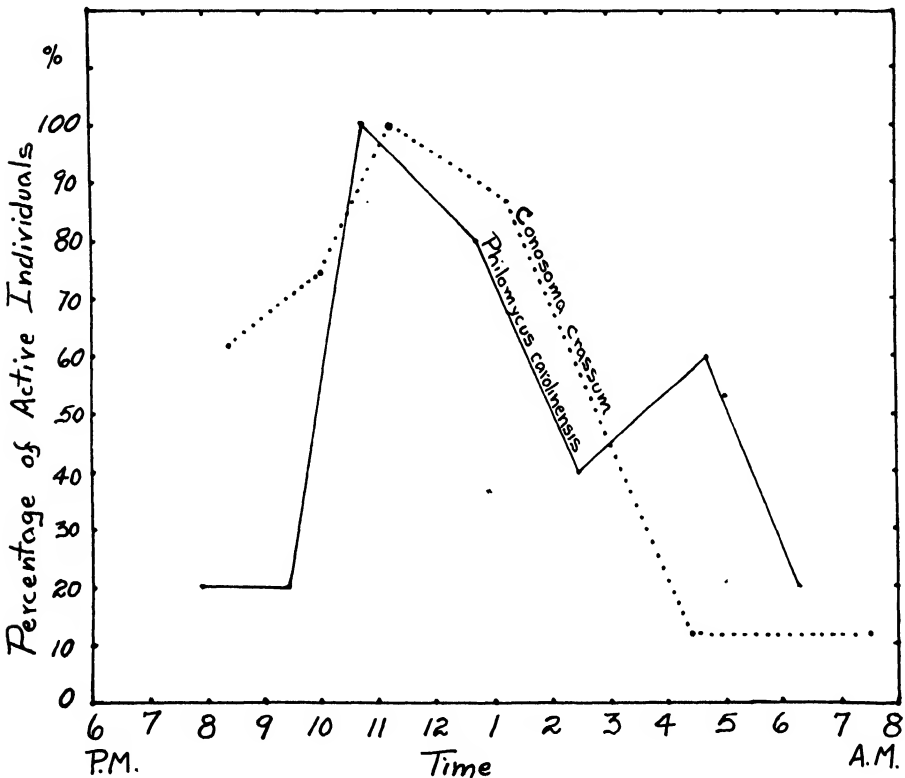


FIG. 1. The activity of nocturnal animals. Staphylinid, *Conosoma crassum* Graves, May 20-21, 1930, Allyn's Woods, Station 31; slug, *Philomycus carolinensis* Bosc., July 11-12, 1930, Haas Forest, Stations 1, 4, 5, 6.

3. Habitat Niches of Nocturnal Animals

The data collected on the 26 species here studied strengthen the conclusion that the forest at night is as important ecologically as the forest during the day. If this is correct, then our knowledge of the forest community must suffer in proportion as this phase of ecological investigation is neglected.

It becomes necessary, therefore, to reclassify some of our ideas concerning the forest fauna, assigning to the nocturnal animals a more prominent position than they have held hitherto. The following outline is tentative, and attempts

to classify nocturnal animals on the basis of their active and inactive periods, especially the nature of their habitat niches.

I. Diurnal species (normally active during the day and inactive at night).
(Subdivisions as below under II.)

II. Nocturnal species (normally active during the night and inactive during the day).

A. Species with their active period spent in the forest and their inactive period spent outside of the forest.

B. Species with the active period outside of the forest and the inactive period within the forest.

C. Typical forest species, viz. species having both their active and inactive periods within the forest.

1. Niche in subterranean stratum. (Fossorial and geocolous species, many myrmecocolous,⁴ termitocolous, etc.).

2. Niche in floor stratum.

a. Dendrocolous (normally having niche in the various stages of the decay cycle of logs and stumps).

b. Mycetocolous (normally seeking shelter and inactivity in fungi and the stages of the fungi decay cycle, Park, '31a).⁵

c. Onthocolous (niche in dung decay cycle).⁵

d. Ptomocolous (niche in carrion decay cycle).⁵

e. Myrmecocolous and termitocolous species, in part.

3. Niche in herbaceous stratum.

4. Niche in shrub stratum.

5. Niche in tree stratum.

III. Diurnal-nocturnal species (species in which some individuals are active through the day and night, e.g. certain forest ants).

The species studied here are typical forest animals, as far as we have been able to determine their active and inactive periods. They have their shelter niches within the floor stratum, and show a well defined nocturnal activity period or periods. Since it has been found that approximately one third of the forest Coleoptera inhabit this level (Park, '31a), during a part of their life cycle, the data on the nocturnal beetles noted becomes especially important.

With accumulation of data, it became apparent that certain individuals regularly frequented particular areas or habitat niches between periods of activity. Although marking experiments would have verified this, the individuals of the carabids studied (*Chlaenius nemoralis* Say, *Galerita janus* Fab., *Platynus hypolithos* (Say) and certain *Harpalus* and *Pterostichini*),

⁴ The term has been defined elsewhere, Park, '29.

⁵ Many species apparently seek temporary shelter in these habitats, having their habitat niches elsewhere, e.g. in the subterranean stratum beneath dung, carrion, fungi, etc. These should not be confused with typical mycetocolous, *et cetera*.

and of the tenebrionid, *Meracantha contracta* (Beauv.), the pyrochroid, *Dendroides bicolor* Newm., and the staphylinid, *Conosoma crassum* Grav. were thought to inhabit each a particular area under the bark of a log or stump, when inactive. Such inactive periods were passed in niches where the bark was loosened by decay and the sapwood moist. These niches were often rather limited in extent, some being 2 to 3 inches in diameter, and the individuals could be observed in them in a relaxed and quiescent condition. Such niche specificity has been suggested previously for certain ground beetles (Park, '30, p. 63), and Boyer and Buchsbaum (see Allee, '31, p. 77) have found marked bees to return at night to the same or nearby flower for their periods of inactivity.

Among the Coleoptera cited above as having niche specificity, a representative example of the data will suffice. A *Galerita janus* Fab. was observed at station 22 in Allyn's Woods. On May 17 it was active at 9:30 P.M., running about on top of the wet bark of the log. At 1:30 A.M. of the same night it had left its niche, and returned at 7:30 A.M. The beetle was watched throughout the following day (11:00 A.M., 1:30 P.M., 4:30 P.M., 6:30 P.M.), but was always found in its niche. At 8:30 P.M. of the following night (May 18) it was again found active on and under the bark adjacent to its habitat. Two days later (May 20) it was found inactive in its niche at 6:15 P.M. It was observed through the night, and, although it became active around 10:15 P.M., it did not move far from its niche, and was still there at 7:20 A.M.

4. Behavior of Nocturnal Species

The nocturnal habit of many species may in part account for their relative rarity in collections, as the animals would be inconspicuous during the day and would leave their niches only late at night. The flattened larvae of the Pyrochroidae are common beneath bark, but the adults are not as well known to collectors as their larvae. The adults may be obtained by chance, or taken at night with light traps, as entomologists know. On July 18 (Station 2, Haas Forest), to mention one case, a female *Dendroides bicolor* Newm. was observed to emerge from its niche under the bark at 9:46 P.M. It was quite active, crawling and flying near the point of emergence. At 11:40 P.M. three other females were found active on the same log. Two were walking back and forth and the third was crawling from its niche under the bark.

Most of the species of Carabidae mentioned are carnivorous. This is especially true of the common Pterostichini, and these (e.g., *Pterostichus adoxus* Say and *Euferonia stygica* (Say)) were numerous at night, crawling actively over the forest floor. The nightly search for prey has been ascribed to other beetles, e.g., the nocturnal cicindelid, *Amblycheila cylindriciformis* Say, as early as 1878 by Riley, *et al.* (p. 315), which is in agreement with other data on nocturnal Cicindelidae, for example, *Tetracha* (Blatchley, '10, pp. 28-29), *Amblycheila* and *Omus* (LeConte and Horn, 1883, p. 3). Other

night-faring species are herbivorous. Thus the carabid, *Harpalus caliginosus* Fab., was studied in the summer of 1925 by the senior author in the Indiana dune region, near Tremont, Indiana. Individuals of this species fed at night, under normal conditions, on the minute black fruits and seeds of the large ragweed, and under experimental conditions upon rose haws and the berries of Solomon's seal. Their activity was greatest between 10:00 P.M. and 4:00 A.M., fell off between 5:00 and 7:00 A.M., and with the full sun, they tended to retire for the day beneath available shelter, where they sprawled with the legs limply stretched out and the body resting on the substratum.

In addition to the predacious pterostichini mentioned above, many mycetocolles were active at night in the forests studied. Some of these lived in the fungi and fed on the fungus tissues or juices at night, and only occasionally were found under bark near by, e.g., *Boletotherus cornutus*. Others were found either associated with the fungi or under bark by day, and frequented the fungi at night, e.g., *Megalodacne heros*. These species were joined by nocturnal carnivores (Carabidae, Staphylinidae) and omnivores (Staphylinidae) which probably preyed on the former (Park, '31a). In Table IV some of the many food relationships of the nocturnal mycetophagous species are listed.

TABLE IV. *Food relationships of certain nocturnal mycetophagous Coleoptera*

Species	Food	Feeding behavior and related data
<i>Agathidium oniscoides</i> Beauv.	<i>Fomes applanatus</i>	Licking fruiting surface of fungus. 8:43 P.M.
<i>Boletotherus cornutus</i> (Panz.)	<i>Fomes applanatus</i>	Very abundant on pileus and fruiting surfaces, feeding and burrowing. 8:30 P.M. to 4:30 A.M.
<i>Leiodes blanchardi</i> Lec.	Myxomycetes: Stemonitis sp.	Feeding all night. On fresh tissues
<i>Megalodacne heros</i> (Say)	Pezizia sp.	Feeding 9:18 P.M.
<i>Ontholestes cingulatus</i> (Grav.)	<i>Polyporus sulphureus</i>	Fungus tissue drying, dull brown, and in stage II of the decay cycle. 7:28 P.M.
<i>Phenolia grossa</i> (Fab.)	<i>Polyporus sulphureus</i>	Feeding all night: 9:37 P.M. to 8:30 A.M.

Another phase of nocturnal activity which should be mentioned here concerns copulation. The mycetocole, *Boletotherus cornutus*, was found to be one of the most active, abundant and typical of the nocturnal fauna, and pairs were commonly observed *in copulo*, or in the mating position, usually from 11:00 P.M. to 1:00 A.M. In one case, copulation was observed as early as 7:12 P.M. Mating in this species is readily discerned since the beetle is medium-sized, and the males usually bear prominent prothoracic horns, and copulatory pads. At times a male would be noted astride the female but with the anterior end reversed, with the head just dorsal to the pygidium of the female. Two females were seen in this peculiar reversed position several times.

The silphid mycetocole, *Leiodes blanchardi* Lec., also copulated freely at

night, as many as 6 pairs being noted *in copulo* between 8:00 P.M. and 4:30 A.M. in one night.

Certain species were found to be active both day and night. Chief of these was the ant, *Aphaenogaster fulva* Roger. Individuals of this species nested in the floor stratum of both forests, and were found active during the day and through the entire night, crawling over moist logs and stumps, fungi and the soil. Similar observations on the nocturnal activity of certain formicids have been made by Flint ('14) on *Lasius niger americanus*. It is to be expected that in such species the periods of inactivity were at different periods for different individuals or groups of workers.

Among the amphibians, *Rana sylvatica* Lec., the climax wood frog, was observed in activity in both forests throughout the night, and at intervals during the day. Other amphibians were found active at night also. Thus individuals of *Plethodon cinereus* (Green) were commonly observed in both forests. Apparently these salamanders passed the day beneath stones and logs and became active by 8:45 P.M., at which time they could be seen occasionally in activity on the tops of stumps, or the forest floor. This general rhythm has been noted by Leydekker ('10, p. 2657). Data was collected which indicated that *P. cinereus* occupied particular niches beneath bark, but marking experiments are necessary before this can be proven.

Another amphibian observed was the spotted newt, *Triturus viridescens* Raf. Individuals in the terrestrial second larval stage were rather common. They were observed in activity but twice, between 7:20 P.M. and 6:20 A.M. Their inactive periods however were very long. One individual inhabited a particular niche in the Haas Forest (station 4), beneath the bark of a small, decayed stump (stage three). Probably the same individual was observed frequently between July 11 and 19, but was noted to have moved but once, a distance of 36 cms. into another niche of the same stump. The nocturnal habits of the species were noted by Pike (1886).

Finally, some of the diurnal forest species were studied at night. Of these may be mentioned the green tiger-beetle, *Cicindela sexguttata* Fab. Individuals were abundant during the day, on the forest floor and paths through the woods. At night the adults were found in niches under the bark of chestnut, maple, and beech logs. In one case, an individual was observed in a niche under the bark of a chestnut log which had been recently felled. The niche was about 2 feet from the floor, bordering a path in Allyn's Woods. When first noted (11:02 P.M., May 24) it was inactive. Its head was lowered on the sapwood, and its legs drawn in against the body. It was not responsive to touch or light from a gasoline lantern or flash-lights. This animal was observed frequently through the night and into the next day (May 25), but no change could be noted in its position nor irritability. The air temperature had been rising from 5° C. at 4:00 A.M. to 16° C. at 1:50 P.M., and the relative humidity dropping from 88 to 48 per cent over the same period. The beetle began slight movements at 1:34 P.M., and had left the niche by 1:50

P.M. At this time the niche temperature was 14° C. Since other individuals were active on the paths before 1:00 P.M., the general period of activity must have begun earlier in the morning. In the case of the beetle noted, the niche temperature probably had been retarded by shade.

5. Correlation of Activity with Environmental Factors

The method employed in gathering data made possible the comparison of nocturnal activity, in terms of numbers of active individuals, with the temperatures, relative humidity and rate of evaporation within a limited period of time. This was found to be essential, as the data indicate that activity at night is closely correlated with the factor complex at a given time. Just how close this correlation is, and to what extent any one factor influences the activity of nocturnal animals was not determined. The ultimate solution of such problems necessarily lies in controlled laboratory work on one or a few species.

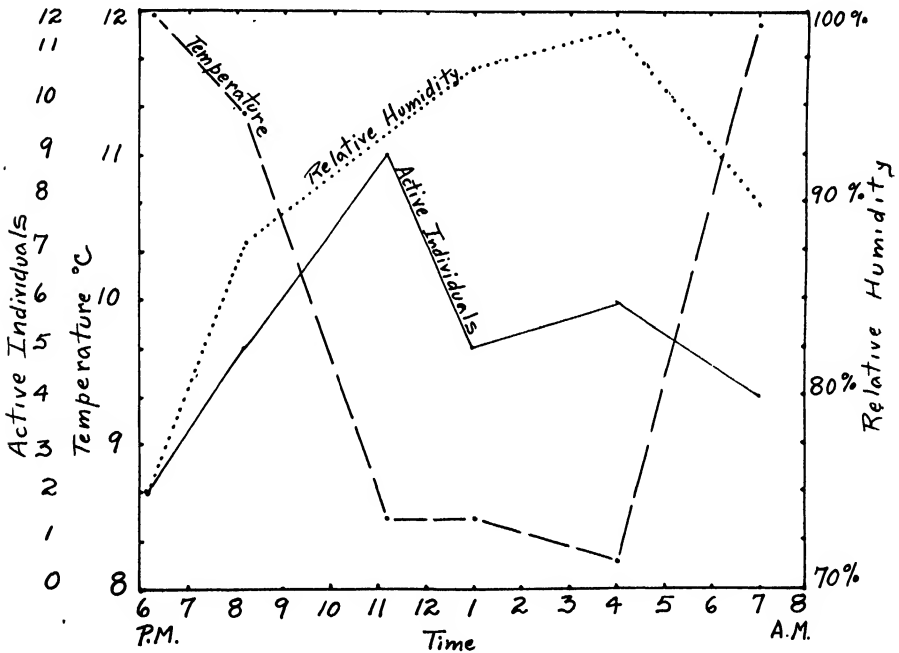


FIG. 2. The nocturnal activity of *Philomycus carolinensis* Bosc., May 20-21, 1930, Allyn's Woods, Hiram, Ohio.

Only a small portion of the data accumulated can be presented here. In the following graphs (Figs. 2, 3, and 4), the air temperature and relative humidity are compared with the number of active individuals of 3 species of nocturnal animals. These data are for one night only (May 20-21, 1930)

and refer to Allyn's Woods, near Hiram, Ohio. The expression of the various environmental factors was taken from the night's complete record at the times when a species was under actual observation at a given station. Thus the temperature curve in any graph does not represent the average temperature throughout the night.

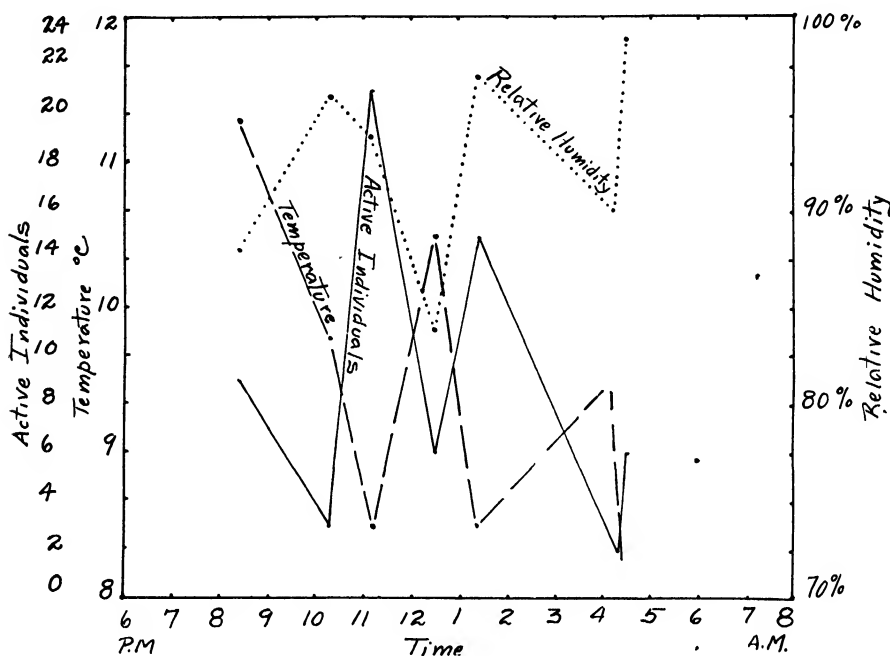


FIG. 3. The nocturnal activity of *Boltotherus cornutus* (Panz.), May 20-21, 1930, Allyn's Woods, Hiram, Ohio.

From these graphs it will be seen that, in general, as the temperature falls and the relative humidity rises, the number of active individuals rises, and *vice versa*. It should be remembered, however, that these factors were operating at night, *i.e.*, in the absence of sunlight. Light may be important in modifying such rhythms, as is indicated by the work of Boyer and Buchsbaum (see Allee, '31, p. 77), in part, and that of Johnson ('26).

The cases of the 3 animals just cited are given as examples. The same general relationship was found to hold for other nocturnal species. This was especially true where sufficient data was collected, and secondly where the instrumental and activity readings fell at the same time. To give one more example, the small silphid, *Leiodes blanchardi* Lec., was observed on 2 nights a week apart. One (July 11-12, 1930) was characterized by high relative humidity and low rate of evaporation and air temperature. The other night (July 18-19, 1930) had low relative humidity and proportionally

high air temperature and rate of evaporation. On these 2 nights the activity of this species followed the general conclusion reached above, namely, activity increasing, up to a point, with rise in relative humidity and fall in temperature (Figs. 5 and 6). The instrumental records were taken 5 feet from the stump where the beetles had their habitat niches (Station 1, Haas Forest).

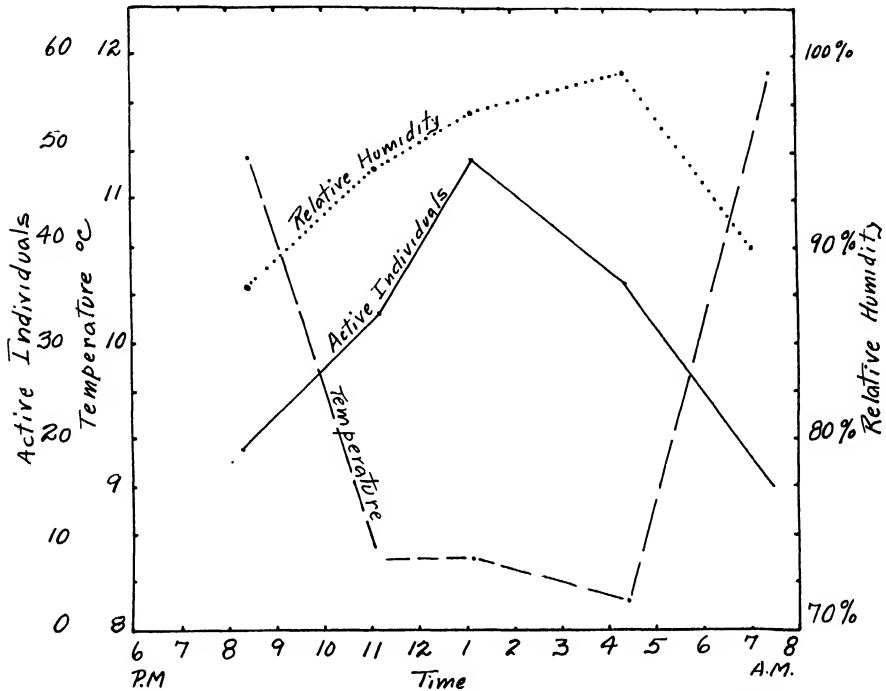


FIG. 4. The nocturnal activity of *Anguispira alternata* (Say), May 20-21, 1930, Allyn's Woods, Hiram, Ohio.

On both nights the observations were made, therefore, on the same set of individuals. The beetles ceased activity (wandering, feeding, copulating) between 8 and 9 in the morning, and crawled into their niches under the bark or in crevices of fungi. They began their activity between 7 and 9 in the evening. It will be seen from the graphs mentioned that the night of July 11-12 was relatively cool and moist, with higher activity, and that the night of July 18-19, one week later, was relatively warm and dry, with practically no activity. Copulation occurred only on the cool, moist night.

From such data we reach the general observation that, for the species studied, and within the limits of the ranges of the factors observed, nocturnal activity tended to increase with increase of relative humidity, decrease of air temperature and rate of evaporation. Conversely, nocturnal activity tended to decrease with decrease of relative humidity, increase of air temperature and rate of evaporation.

This conclusion refers to the activity of the animals observed between air temperatures of 8 to 28° C., and relative humidities of 75 to 99 per cent. The evaporating power of air has been emphasized by Shelford ('14 a, b) as affecting animal behavior. All of these factors probably play a part here. Since the species studied were poikilothermic it is obvious that the conclusion stated would not hold for a temperature complex beyond the limits of toleration.

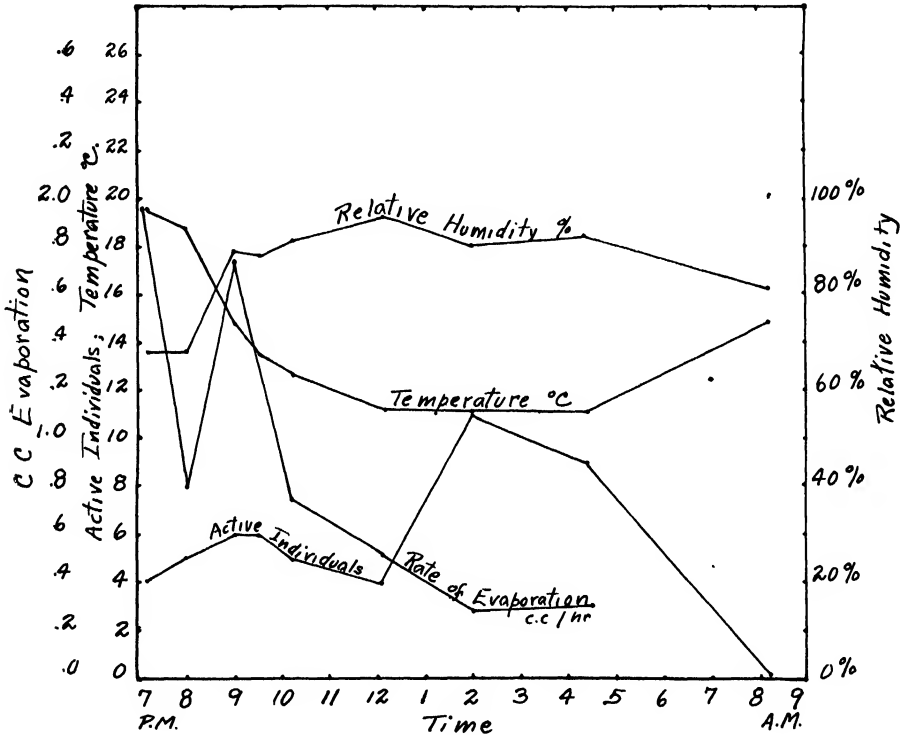


FIG. 5. The nocturnal activity of *Liodes blanchardi* Lec., Haas Forest, July 11-12, 1930. Relatively cool and moist.

It should be noted that the observed activity of these nocturnal species is given when the factors measured are in the usual nocturnal phase of their cycle. Consequently it must be shown experimentally that the factors of the environment do control the nocturnal activity rhythm, although the data given here on *Leiodes blanchardi* Lec. indicate that this is probable at least for certain species. It is probable that the nocturnal rhythm is inherent, rests upon physiological requirements, and expresses itself when the factor complex is favorable.

Pierce ('16) working with the cotton boll-weevil, graphed the optimum relative humidity for the species between 60 and 70 per cent. However,

Chapman ('26, p. 97) thinks that this optimum would be closer to 100 per cent for most insects, which, in view of the nocturnal beetles observed, would appear to be more justified.

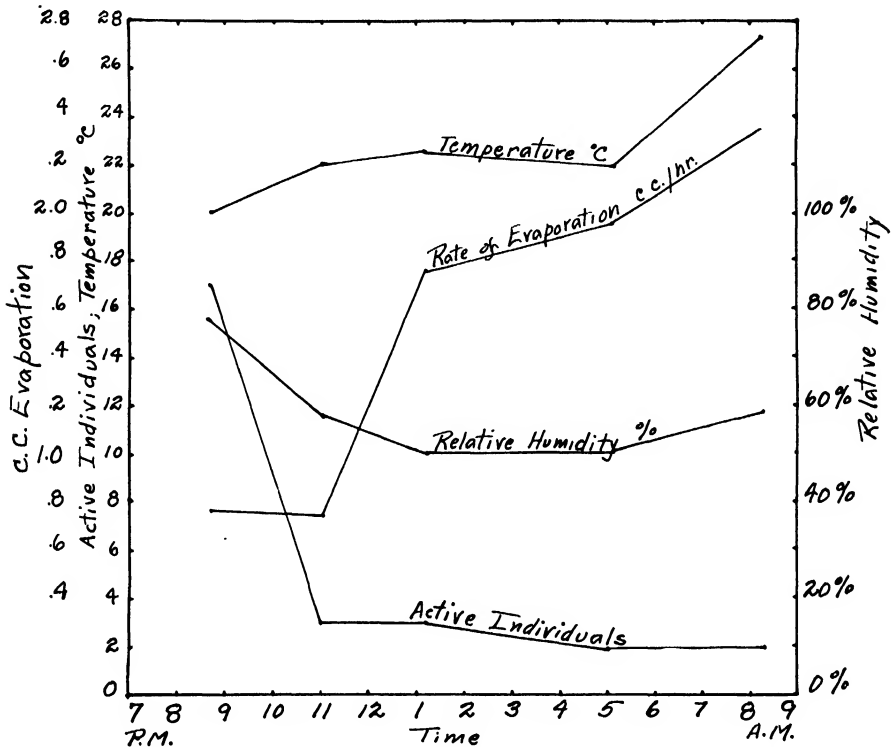


FIG. 6. The nocturnal activity of *Liodes blanchardi* Lec., Haas Forest. July 18-19, 1930. Relatively warm and dry.

DISCUSSION OF DAY AND NIGHT RHYTHMS

It is well known to field workers that many normally diurnal insects are attracted to artificial lights at night (Howard, 1899; Houghton, '05; Frost, '15; McIndoo, '26), and that cloudy days are different from bright days with respect to the distribution and activity of insects (Chapman, *et al.*, '26; Allard, '30). Fiebrig ('12), recognizing the physiological similarity between sleep in the higher vertebrates and in insects, found, among other characteristics of sleep, that there is an adjustment of sleeping periods to the changing periods of night and day. Turner ('11), discussing the behavior of certain parasitic bees, found that the bees would retire to the cells of the host at night, or when the room was darkened.

Many Mordellidae (*Mordella marginata* Melsh.), Coccinellidae (*Coccinella novemnotata* Hbst.), Buprestidae (*Acmaeodera pulchella* (Hbst.)), and the anthocolous cerambycids (*Typocera velutina* (Oliv.) and the Lep-

turoid species) among beetles, frequently are found in herbaceous foliage or upon flowers, as late as 9:30 A.M. in mid-July in an inactive and quiescent condition in the Chicago area. This period of inactivity is prolonged on overcast days. When such forms are disturbed they respond slowly at first. Some moments later, if repeatedly disturbed, they regain normal activity and fly or crawl away. On clear, bright and warm mornings such species promptly letisimulate (feign death) or fly off when so disturbed.

With respect to the autecology of diurnal species at night, considerable data have been gathered, *e.g.*, Soule, 1888; Schwarz, 1896; Banks, '02, '08; Brues, '03; Rau and Rau, '13, '16; O'Byrne, '30; Hayward, '30; Cook, '30, and Allee, '31, pp. 74-79, to mention a few of the many workers in this field. Some of the points brought out by these and other investigators can be summarized briefly: (1) Insects frequent certain habitat niches more than others for periods of inactivity. (2) Insects appear to have characteristic attitudes while inactive. (3) Insects are difficult to arouse from this inactive condition. (4) Insects are often gregarious, forming sleeping aggregations. (5) The condition of sleep, or its physiological equivalent, is known for various groups of insects.

Such periods of inactivity are physiologically necessary for most if not all species, and the biological advantages accruing from a nocturnal activity cycle are obvious when so many animals spend the night in a quiescent condition. Of these may be mentioned the less alert condition of the inactive prey for nocturnal predators (Floersheim, '06; Borradaile, '23, p. 88). Even the advantageous adjustment of certain parasites to their hosts (Fasten, '13) may be mentioned in this connection. It is to be expected that many typical nocturnal species would show more or less physiological and morphological, as well as ecological adjustment to such a rhythm.

As yet the nature of such rhythms is not understood. They may be internal, or partially or wholly regulated by the environmental complex. Among the possible factors initiating day-night periodicity, the relative length of day and night throughout the year may be mentioned. There is sufficient data on photoperiodicity to strengthen this possibility (Garner and Allard, '20; Rowan, '26; Kellerman, '26). Daylight intensity is another possible factor, the importance of which is as yet undetermined. It has been shown that the daylight intensity follows a rhythmic seasonal, and daily cycle in forests (Park, '31 *b*). Such changes, however, obviously are correlated with changes in the other factors operating, *e.g.*, temperature and humidity. That the day-night rhythm is more or less modifiable by the environment is indicated by the work of Johnson ('26) on the modification and reversal of activity in nocturnal forest deer mice.

In conclusion, then, it would appear that careful investigation of day-night periodicity of animals has only begun from an ecological point of view. Further, it is felt that the nocturnal fauna must be much more thoroughly evaluated before our knowledge of the community can be considered complete.

SUMMARY

Observations were made on the ecology of nocturnal animals of two beech-maple forests in northeastern Ohio, and a classification of forest animals suggested, based on their periods of activity and inactivity and the habitat niche.

The data presented indicate that: (1) nocturnal species have a definite rhythm of activity, being active at night and inactive by day; (2) the average range of activity is between 8:23 P.M. and 4:41 A.M.; (3) the maximum activity occurs usually towards the middle of the night, between 10:00 P.M. and 2:00 A.M.; (4) certain species are inactive in particular niches of their habitat.

Data are presented on the behaviour of nocturnal animals, *e.g.*, food relationships, shelter rhythms, and copulation, and the general problem of day-night periodicity is discussed.

The general conclusion is reached that for the species studied, and within the ranges of the factors observed, nocturnal activity tends to increase with increase of relative humidity, decrease of air temperature and decrease in rate of evaporation. Conversely, activity of nocturnal species tends to decrease with decrease in relative humidity, increase of air temperature and increase of evaporation rate.

It is held that the nocturnal fauna must be evaluated before our knowledge of the community can be considered complete.

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TEMPERATURE RELATIONS OF LODGEPOLE-PINE SEED GERMINATION ¹

FERDINAND W. HAASIS ² AND ADRIAN C. THIRUPP ³

Introduction

During the winter of 1927-28 a series of seed germination studies was made by one of the authors at the Laboratory of Plant Physiology of the Johns Hopkins University, with the object of ascertaining the optimal maintained temperature for the occurrence of germination, and other temperature relations of the seeds studied. In these experiments it was observed that, for short incubation periods (6-7 hours), the optimal maintained temperature for a certain lot of pitch pine (*Pinus rigida* Mill.) seeds was about 46° C. (see Haasis ('28)). For relatively long periods (4-14 days) the optimum was about 25-33°, the upper limit being lower for the longer periods.

For intermediate lengths of incubation period, there was a pronounced double optimum, about 33° and 43°. The highest temperature at which germination of these seeds occurred was 57° C. Somewhat similar relations were found in studies of some other lots of coniferous-tree seed. The one lot of rice (*Oryza sativa*) seed available, on the other hand, while showing complete germination at certain temperatures, failed to germinate at the temperatures employed above 42°, i.e., 45°, 48°, 51°, and 55°, and did not show the phenomenon of a double optimum for the occurrence of germination.

In view of the temperature relations brought out by these studies, it seemed desirable to extend them to an investigation of the behavior of seeds of an individual species produced under diverse climatic conditions. It was believed that such a study might throw some light on the reasons for unsatisfactory performance of plants grown in other localities than those in which the seeds were collected, and perhaps on the relations of varieties and the evolution of new species. Collections of seeds of lodgepole pine (*Pinus contorta murrayana* (Balf.) Engelm.) made in 1927 in a number of localities in British Columbia seemed to afford a good opportunity for such a comparative test.

Of the several causes of variation in local climatic conditions, those dependent on differences of latitude and altitude are probably the most important. Seeds may be collected from different climatic regions extending over several degrees of latitude at nearly the same elevation or at different

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altitudes in the same general locality. In the latter case, to mention one of the many factors which are operative, the intensity of the solar radiation reaching the site would unquestionably vary, being greater at the higher altitudes. This latter effect would often be again modified by the frequently greater precipitation and cloudiness at the higher elevations. In the case of climatic differences dependent upon differences in latitude, the variation in the length of day might be of significance in addition to the actual differences in temperature. Especially in connection with germination, the length of day may be of considerable importance because of its influence on the time during which the germinating seeds are exposed to exceptionally high temperatures.

It was thought possible, before the germination tests were made in the current study, that the seeds from the lower elevations might need higher temperatures for rapid germination than the seeds from the higher elevations, since the ancestors of the former had been used to higher year-round temperature averages. In addition, it was thought that perhaps the optimal temperature for the low-elevation seed might be higher than that for the seed from the higher elevations, and also that the seed from the high elevations might respond more quickly to the lower maintained temperatures.

Description of Seed-Collection Localities

The seeds used in this study were collected in six different localities in British Columbia, ranging from 350 to 1,500 meters (1,200 to 5,000 feet) above sea level, and for the most part within 30 minutes of latitude, as follows:

Lot 2.⁴ Shuswap Lake. 350-450 m. (1,200-1,500 ft.), 50° 46'-51° 00' N.

Lat., 119° 00'-119° 30' W. Long.

3. Mount Ida. 900 m. (3,000 ft.), 50° 36' N., 119° 16' W.

4. Highland Valley. 1,200 m. (4,000 ft.), 50° 29' N., 121° 00' W.

5. Long Lake. 1,300 m. (4,200 ft.), 50° 30' N., 120° 30' W.

6. Barnes Creek (Nicola National Forest). 1,300 m. (4,200 ft.), 50° 40' N., 121° 06' W.

7. Upper Hat Creek. 1,500 m. (5,000 ft.), 50° 32' N., 121° 36' W.

The locations of these points are shown on the accompanying sketch map, figure 1. The physical conditions, so far as known, are briefly summarized on page 730.

Descriptions of all the precise areas where the seeds were collected are to be found in a paper by Ilvessalo ('28, pp. 8-11), with the exception of the collection sites for Lots 2, Shuswap Lake, and 7, Upper Hat Creek. Ilvessalo lists the native vegetation of the several areas on pages 94 to 111. His de-

⁴ Lot 1 is used to designate seed of the 1927 crop purchased from C. B. Fleu, Jr., of Philadelphia, Pennsylvania, in January, 1928. The origin of this seed is not known. The results of some experiments with it have been reported by Haasis ('28).

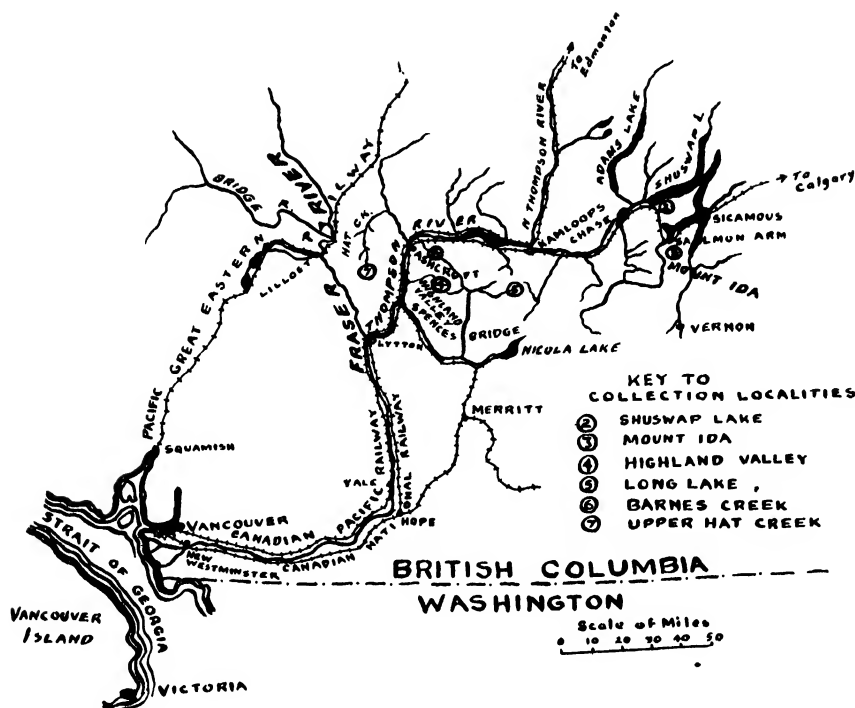


FIG. 1. Sketch map showing collection localities for six lots of lodgepole pine seed

Locality	Annual precipitation, mm.	Temperature. Degrees, Centigrade *							
		Mean				Extreme			
		June	July	Aug.	Sept.	June-Sept.	Year	Max.	Min.
Shuswap Lake.....	500-530	15.5	19.0	18.0	12.0	16.0	7.0	38.0	-34.5
Mount Ida.....	635	13.0	16.5	15.0	10.5	13.5	4.5	36.5	-37.0
Highland Valley.....	381	11.5	15.5	14.5	10.5	13.0	4.0	36.0	-43.0
Long Lake.....	457	11.0	15.0	14.0	10.0	12.5	3.5	34.5	-43.0
Barnes Creek.....	406	10.0	14.5	13.5	9.5	12.0	3.0	34.5	-43.0
Upper Hat Creek.....	381	8.5	14.0	13.0	7.0	10.5	1.5	32.0	-45.5

* Temperatures for Shuswap Lake are from the records for Salmon Arm, elevation 350 m. At 450 m. the annual mean is probably slightly lower. The temperatures given for the other localities are not from records made at the localities themselves but are interpolated from records at similar altitudes in other parts of the province.

Locality	General character of		
	Bed rock	Soil	Subsoil
Shuswap Lake. . .	Mica schists and shales	Silty clay loam	Glacial till with beds of clay
Mount Ida.	Basalt	Sandy silt loam	Glacial till and disintegrated basalt
Highland Valley. .	Granite	Gravelsand sand with some silt	Glacial gravels with many large boulders
Long Lake.	Basalt	Silty loam	Unsorted glacial till with considerable clay
Barnes Creek. . . .	Basalt	Silty loam	Unsorted glacial till with considerable clay
Upper Hat Creek. .	Marble	Gravelly loam	Glacial till with many boulders

scription of the area "Near Sicamous railway station" (p. 11) is typical for the Lot 2 site. The seeds of Lot 7 were collected in a place where the conditions are very similar to those for Lot 4, but at a higher elevation, where, on the poorer sites, *Arctostaphylos uva-ursi* is often replaced by *Empetrum nigrum*.

The Shuswap-Lake seed (350-450 m.) was collected from trees growing about 150 m. above the lake. This area is in an apple-growing region where the snow lies on the ground from about the first of December until the middle or end of March. The precipitation curve shows two marked maxima, the first one in June, the second between November and January. The weather is very dry in July and August, and again in March. The winters are occasionally severe. In 1924-1925, for instance, the temperature dropped in 10 hours from 12° C. above zero to 29° below. At this time a strong north wind was blowing and the ground was bare of snow. As a result, in exposed places many buds were killed, including buds of young Douglas fir trees.

The following trees are found in the forests of this section: Douglas fir (*Pseudotsuga taxifolia*), western white pine (*Pinus monticola*), western red cedar (*Thuja plicata*), western larch (*Larix occidentalis*), and western birch (*Betula occidentalis*), with a little Engelmann spruce (*Picea engelmanni*), aspen (*Populus tremuloides*), western hemlock (*Tsuga heterophylla*), western yew (*Taxus brevifolia*), cottonwood (*Populus trichocarpa hastata*), alder (*Alnus tenuifolia*), and Rocky Mountain maple (*Acer glabrum douglasii*).

The vegetation of both this and the following locality affords examples of Thrupp's "pachystima forest type" ('27). Although the Shuswap Lake area is lower than Mount Ida, no great difference in the lodgepole pine should be expected, since the species in the former region is to a large extent a migrant from the higher elevations. Only comparatively young stands, which have come in after fire, are to be found on the lower area around Shuswap Lake, and there are few old trees.

The vegetation of the Mount Ida area, with its slightly cooler climate and slightly greater precipitation, is much the same as that of the Shuswap Lake vicinity except for a greater abundance of grass. Lodgepole pine in the Mount Ida area almost always constitutes a temporary type, replacing Douglas fir, western white pine, and western red cedar forests after fire.

In the Nicola National Forest, south of Ashcroft, lies Highland Valley, well sheltered from the north and west winds. It is drier and has higher temperatures than the Barnes Creek area, which is fully exposed to the cold northerly winds. The soil generally is very poor. For the most part, the forest belongs to the *Arctostaphylos* or *Arctostaphylos-Calamagrostis* type, as described by Thrupp ('27).

In the Long Lake Forest area lodgepole pine does not, in general, occupy much land that could not support other species. For the most part it composes a temporary type replacing other species after fires, Douglas fir at the lower elevations, and Engelmann spruce and alpine fir (*Abies lasiocarpa*)

higher up. The forest type here is different from that in Highland Valley and is for the most part in the *Calamagrostis* type (Thrupp, ('27)). There is very little in the drier *Arctostaphylos* type and not much in the *Arctostaphylos-Calamagrostis* type except on southern or western slopes, or where the soil is markedly gravelly or sandy. The general picture of the vegetation shows a large number of species dominated by pine grasses (*Calamagrostis*) in the younger forests, which are replaced more or less by blueberries (*Vaccinium* spp.) and mosses as the stand grows older.

The Barnes Creek area is a poorer site than Long Lake Forest but slightly wetter, on the average, than Highland Valley. The vegetation is for the most part of the *Calamagrostis-Arctostaphylos* type, with blueberries and mosses in the older stands.

In the Upper Hat Creek area the vegetation is mostly of the *Arctostaphylos* type, with the *Calamagrostis-Arctostaphylos* type to a limited extent on the better soils.

Experimental Methods

The germination methods used were essentially the same as those described by Haasis ('28), except that in these lodgepole pine tests only 50 seeds were used to a culture. These seeds were soaked for an hour at room temperature in an antiseptic solution (composed of one gram of "Semesan" powder⁵ to 400 milliliters of water), planted on agar gel (25 ml. of a solution made up of one gram of "Bacto-Agar" to 100 ml. of water) in covered glass Petri dishes (1 by 9 cm.), and incubated at various maintained temperatures, a battery of 7 maintained-temperature chambers being used. With agar gel of this composition in such covered dishes, the air directly above the seeds was undoubtedly very nearly or quite saturated with water vapor during the experiments, except for the brief periods when observations were being made. The agar serves to solidify the water, thus eliminating the risk of the seeds becoming submerged and so having the oxygen supply reduced, but leaves ample water available for the germination processes.

The tests were continued for not longer than 7 days, observations of the percentage of germination being made periodically, usually at one-day intervals. In these studies germination was considered to have occurred when the tip of the primary root had protruded beyond the edges of the ruptured seed coat.

These germination tests were made in the spring of 1928, while the first-named author was an assistant at the Laboratory of Plant Physiology of the Johns Hopkins University.⁶ The time available for this study was insufficient for adequate duplicate tests, and the records obtained are limited to

⁵ "Semesan" powder is stated by Doctor W. H. Tisdale to contain 35 per cent, by weight, of hydroxy-mercuri-chloro-phenol, the balance being about one-third Ca CO_3 and two-thirds $\text{Na}_2 \text{CO}_3$.

⁶ Grateful acknowledgment is hereby made to Doctor Burton E. Livingston, director of the Laboratory of Plant Physiology, for helpful criticism of the manuscript of this paper.

TABLE I. *Percentages of germination for six lots of seeds of Lodgepole Pine, at seven maintained temperatures, for various periods of incubation*

Temp. ° C.	Lot no.	Percentage of seeds germinated at end of period of:							
		6 hrs.	1 day	2 days	3 days	4 days	5 days	6 days	7 days
15	2	0	4	4	6	6	10	10	16
	3	0	4	4	4	4	8	10	12
	4	0	0	0	0	0	0	2	2
	5	0	0	0	2	4	6	6	8
	6	0	0	0	0	2	2	2	6
	7	0	0	0	2	2	6	6	12
19	2	0	4	4	4	10	18	28	36
	3	0	6	18	20	26	32	40	56
	4	0	0	0	0	12	22	32	52
	5	0	0	0	0	4	18	36	46
	6	0	0	0	2	16	42	60	72
	7	0	0	0	4	34	56	74	80
24	2	0	4	8	26	52	72	82	90
	3	0	6	10	24	38	66	78	78
	4	0	0	0	18	54	78	84	90
	5	0	0	0	20	54	76	84	88
	6	0	0	2	18	62	82	86	90
	7	0	2	8	38	74	82	86	86
27	2	0	0	10	56	78	86	88	90
	3	0	2	20	44	66	78	82	82
	4	0	0	10	56	68	86	88	88
	5	0	0	8	42	64	76	82	86
	6	0	2	8	42	64	74	78	80
	7	0	0	18	54	70	76	76	76
33	2	0	6	28	46	50	56	60	60
	3	2	10	30	54	60	68	68	68
	4	0	0	0	20	32	36	40	46
	5	0	2	12	28	34	38	52	54
	6	0	2	14	22	36	44	—	—
	7	2	2	12	32	42	50	—	—
36	2	6	18	44	48	58	60	62	62
	3	8	28	46	56	60	66	68	74
	4	0	4	10	22	30	34	40	44
	5	0	4	14	20	22	28	40	42
	6	0	4	12	22	30	34	—	—
	7	2	10	26	30	34	40	—	—
41	2	10	66	76	80	80	82	82	82
	3	4	44	58	62	64	64	64	64
	4	0	22	32	32	32	32	32	32
	5	0	18	22	36	40	40	40	40
	6	6	16	18	18	18	18	—	—
	7	6	26	30	32	34	34	—	—

observations of a relatively small number of cultures. Nevertheless the results appear to be worth recording as suggesting what may be expected from more thoroughgoing studies of this sort.

The maintained temperatures used in this study were the following: 15°, 19°, 24°, 27°, 33°, 36° and 41° C. (59°, 66°, 75°, 81°, 91°, 97° and 106° F.)

At each of these temperatures one seven-day test was made of each lot of lodgepole pine seed, except for lots 6 and 7, for which five-day records were procured for temperatures 33°, 36° and 41°.

Results and Discussion

The percentages of germination for various periods of incubation are shown for each of the six lots of seed in Table I, and graphically in figures 2-7.

EARLY GERMINATION AT HIGH TEMPERATURES

It will be observed that in all cases the greatest percentage of germination at first, in one day or less, was at relatively high temperatures, 36° or 41° (97° or 106° F.). That is to say, for these short periods the most favorable temperature for the occurrence of germination was above 33° C. and usually at least as high as 41°.

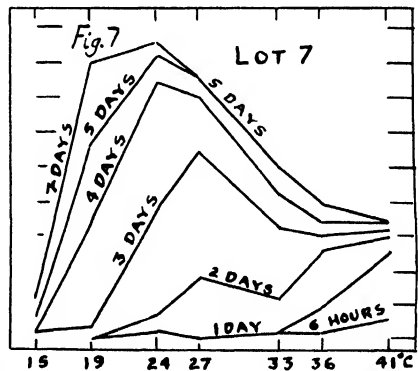
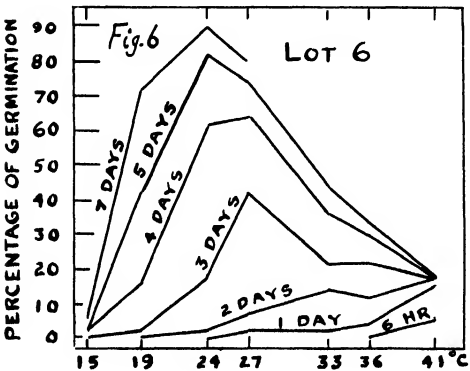
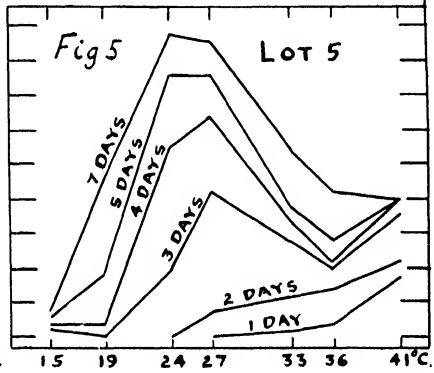
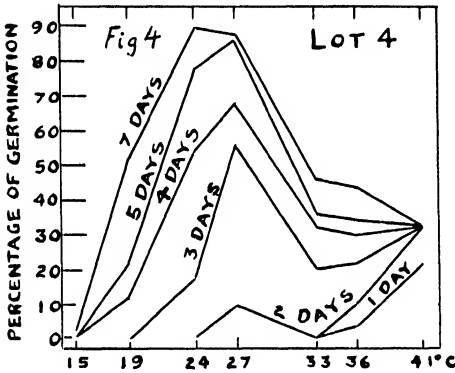
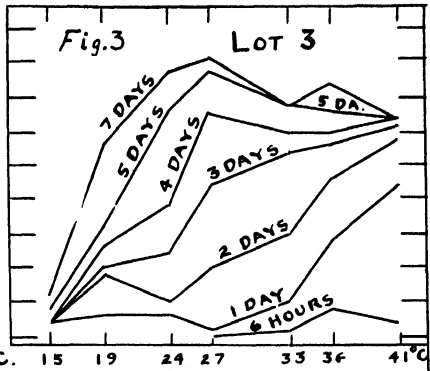
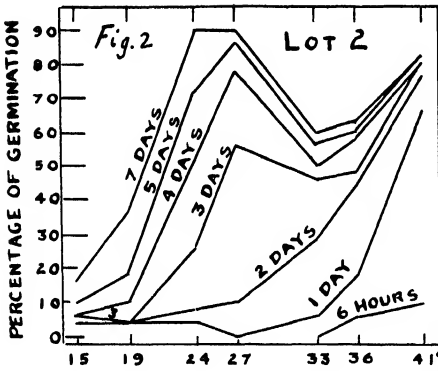
DOUBLE OPTIMUM

For longer incubation periods the optimal temperature for the occurrence of germination was lower, but not progressively so in a regular sequence for each lot of seed. There is a temperature around 33° and 36° C. at which germination occurred rather tardily for all the lots, none of the optima being found there. The result is that some of the sets of observations show double optima, as can be seen, for example, in the 3-day graphs for Lots 4 and 5, the 4-, 5-, and 6-day graphs for Lot 2, and the 4- and 7-day graphs for Lot 3. In Lots 6 and 7 the double optimum would have been evident had figures been available for 2.25- or 2.5-day incubation. This would be less pronounced in the case of Lot 6 than for Lot 7.

Both these phenomena, the early germination at high temperatures and the double optimum for the occurrence of germination, agree with the previously reported results referred to in the early part of this paper. They held true for lodgepole pine seed purchased commercially (Lot 1) as well as for several lots of seed of other conifers.

CORRELATIONS BETWEEN TEMPERATURE OF COLLECTION SITE AND EXPERIMENTAL OPTIMUM

Considering the results for all six lots of our seed, temperature by temperature, for the 5-day period, it is evident that there are certain trends which are apparently connected with climatic differences in the native sites of the seeds. Such a comparison is shown in figure 8 where the germination indices for each lot of seed are calculated as percentages of the maximum germination obtained with that lot. While this method improves the perspective, making the comparison of results somewhat easier than the use of mere percentages of germination, yet it is to be borne in mind that these maxima



FIGS. 2-7. Temperature-germination graphs for lodgepole pine seeds, lots 2, 3, 4, 5, 6 and 7 (from elevations of 350-450, 900, 1,200, 1,300, 1,300 and 1,500 meters respectively), for 6 hours, and for 1, 2, 3, 4, 5 and 7 days of incubation. Each percentage is based on but a single culture.

are not necessarily the maxima obtainable with these lots of seeds. It is conceivable that had other temperatures been used than the seven actually employed, the germination percentages might have been greater than actually disclosed.

In these graphs it will be seen that the seeds from the highest elevations showed much better germination at the low temperature of 19° than the seeds

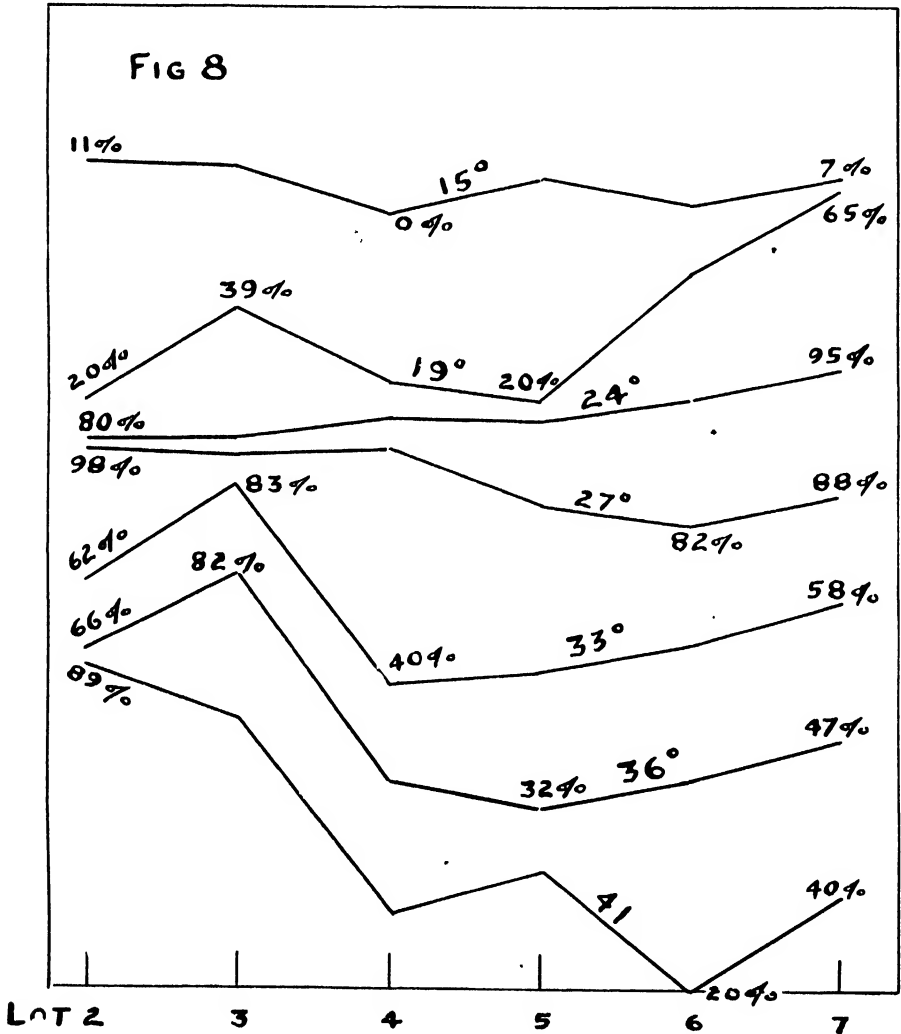


FIG. 8. Graphs showing germination at each of 7 maintained temperatures for 6 lots of lodgepole pine seeds, incubated 5 days. Each graph represents a particular temperature as indicated on the graph, for all lots of seed, indicated at the bottom of the figure. Germination indices, that is, percentages of the maximum germination observed for each lot of seed in a 7-day incubation period, are given for the seeds from the lowest and highest elevations (Lots 2 and 7) and for high and low points on the graphs.

from the lower elevations (and higher native temperatures). At the highest temperature used, 41° , on the contrary, the seeds from the lowest elevation showed much better germination than those from the highest elevation. For the temperatures between these two extremes, the results were intermediate with an approximate gradation from one to the other. Although the results at 15° are not harmonious with those at the other temperatures studied, yet it is suggested that the seeds of a species from the colder parts of its range may be expected to respond more quickly to low temperatures (provided they are not too low) than those from warmer regions, while those from the warmer climate are likely to germinate more promptly at higher temperatures.

In spite of the small number of observations, the six lots of seed show themselves to have been fairly uniform in germination under the more favorable conditions, the maximum germination percentage varying for the several lots from 82 to 90, and the differences appearing are accordingly much more significant than if the several lots had shown marked differences in germination under favorable conditions.

With regard to the 1-day germination it is perhaps significant that the seeds of Lot 2 show a pronouncedly high percentage of germination (66) at 41° as compared with those of Lot 7 (26). The percentage values for this 41° germination do not conclusively show a regular gradation from the 360-m. seed to the 1,500-m. seed, though the few figures available do suggest such a relation, as shown below:

Percentages of germination for one-day incubation period at 41° C. (106° F.)

	Actual	Based on maximum 7-day germination in each lot
Lot 2 (360-450 m.).....	66	73
Lot 3 (900 m.).....	44	54
Lot 4 (1,200 m.).....	22	24
Lot 5 (1,300 m.).....	18	20
Lot 6 (1,350 m.).....	16	18
Lot 7 (1,500 m.).....	26	30

In figures 9 are assembled graphs for the 5-day germination of all six lots of British Columbian seed at all temperatures tested. It will be seen that there is no uniformity in the relative positions of the values for the several lots at the various temperatures. Indeed there is scarcely more variation than might be expected in one lot of seed.

This fact may perhaps be brought out more clearly by comparing figure 9 with figure 10, which shows 5-day graphs for pitch pine (*Pinus rigida*) seed for a set of maintained temperatures covering about the same range as those used in the present lodgepole pine study. The middle graph is based on average values, the number of 100-seed cultures upon which each point is based being indicated near its plotted position. The other graphs, broken

lines, join points which represent the maximal and minimal values, respectively, for each of the maintained temperatures. It will be observed that, while there is somewhat more spread, temperature by temperature, in the graphs for the British Columbian lodgepole pine seed than in those for the New Jersey pitch pine seed, yet the points for any one lot of lodgepole pine seed do not occupy consistent positions relative to the others.

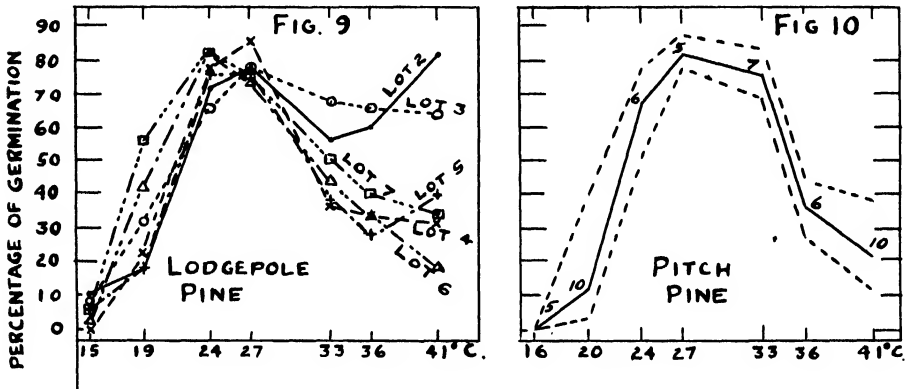


FIG. 9. Combined temperature-germination graphs for 5-day incubation period for lodgepole pine seeds, lots 2-7.

FIG. 10. Temperature-germination graphs for 5-day incubation period for pitchpine seeds collected in New Jersey in 1926. The full line represents average values, the number of cultures upon which each value is based being indicated near the plotted points. The broken lines join points which represent maximum and minimum values respectively for each of the maintained temperatures.

It is to be observed in this connection that the pitch pine seed here considered (Lot 1, as described by Haasis ('28)) was reported by the dealer as collected simply "in New Jersey," without distinction as to any differences there may have been between the sites upon which the parent trees were growing. While the differences in elevation in New Jersey are not as extreme as in the series of British Columbia sites, a collection of seeds from such a general region might well include seeds produced on appreciably different soils and possibly in somewhat different climates. The extreme differences due to soil, altitude, and climate combined would be represented by points at sea level near the southern end of the state and at points at an elevation of around 600 m., 2° farther north. In the study of pitch pine seeds, Haasis found the seeds of different lots behaved somewhat differently from those of Lot 1, almost as differently as would have been expected of seeds of another species. This may, of course, have been due to differences in maturity of the seed at the time of collection or to various conditions of storage. It must also be considered possible, however, that such differences are to be attributed to the fact that the several lots were made up chiefly or wholly of seed produced under diverse climatic conditions.

SIGNIFICANCE IN AFFORESTATION PRACTICE

Studying 10- to 13-year-old pine plantations in Sweden, Eneroth ('26) has found a well-marked correlation between the survival of planted trees and the mean temperature of the planting site as compared with that of the locality in which the seeds were produced. He sums up the significance of the points brought out by this study as follows: "If we use pine seed from a locality the mean temperature of which for the months of June-September or of September, respectively, is 1° C. higher than the mean temperature of the planting-field, we encounter the probable risk that the result of the planting will be 35 per cent or 27 per cent less respectively than it would have been if the seed were gathered on the spot; this difference in mean temperature being caused either by difference of latitude, difference of height above the sea level, or a combination of both" (p. 61).

Apparently with these studies in mind (see Hanzlik ('28)), the Swedish Forest Service has prepared a set of instructions for forest supervisors. These provide that pine seed from various regions shall be kept separate. A list of zones has been prepared as a guide in this segregation, Zone 1, 0-100 m., Zone 2, 100-200 m., Zone 3, 200-300 m., etc. It is required that when seeding is done the difference between the normal temperature of the seeding area and that of the place where the seed was grown shall not be more than 0.5° C.

The indications of the present study, already noted, that seeds from the cooler climates germinate better at the lower temperatures than seeds from the warmer regions, afford evidence in support of Eneroth's thesis so far as germination is concerned; though it is to be borne in mind that germination is not the only thing to be considered in afforestation.

COMPARISON OF RESULTS WITH RESULTS OF OTHER GERMINATION TESTS

It is interesting to compare the results obtained in the present study with those reported for lodgepole pine by Rafn ('15) for tests made in Denmark, and by Toumey and Stevens ('28) for tests made in Connecticut, which are here listed in Table II. It will be observed that Rafn's percentages are markedly lower for a 5-day period than ours at most of our incubation temperatures. On the other hand they are appreciably higher for a given length of time than Toumey and Stevens's. Perhaps this latter divergence is partly due to the fact that most of the tests reported by Toumey and Stevens were made in soil, while Rafn's were made in a Jacobsen germinator. Because of the lapse of time before the germinated seedling appears above the soil, germinator percentages are apt to be higher than soil percentages (cf. Toumey and Stevens, '28, p. 17), but the differences due to this cause would hardly be so great as is shown by the figure of Table II. It is of course entirely possible that the poor germination reported by Toumey and Stevens may have been related to low vitality of their seeds, which in turn may have been dependent upon the conditions of their production and storage.

TABLE II. *Percentages of germination of Lodgepole Pine seed, after various periods of incubation (Rafn ('15) and Toumey and Stevens ('28))*

		Days of incubation									
		5	10	15	20	25	30	35	40	45	50
Rafn (11 tests; seed from Rocky Mountains)	Maximum....	10	64	—	92	—	92	—	—	—	—
	Average.....	1	31	—	69	—	83	—	—	—	—
	Minimum.....	0	0	—	42	—	68	—	—	—	—
Toumey and Stevens (9 tests; seed from Pacific Coast and Rocky Mountains)	Maximum.....	—	—	5	6	7	8	9	12	24	24
	Average.....	—	—	1	2	3	3	3	4	10	11
	Minimum.....	—	—	0	0	1	1	1	1	3	4

SIGNIFICANCE OF INCUBATION TEMPERATURE

With these considerations before us, we may turn our attention to the temperatures used in the tests, an influencing condition which can not be ignored. In the Connecticut tests the air temperature fluctuated between 10° and 27° C. (50° and 80° F.), the soil temperature at 5 cm. varying from 14° to 22° (57° to 72° F.). The temperatures actually used in the Danish tests are not specifically stated, but the maximum, judging from a citation of Toumey's ('16, p. 119). from I. Jacobsen (Keimprüfung von Waldsamen, Centralblatt f.d. gesamte Fortwesen: 22-28, 1910) was presumably about 25-28° C. Elsewhere (see Gevorkiantz, '28), Jacobsen is cited as recommending a temperature of 20°-30° C. Probably it is here that one significant cause of the difference between the two sets of tests is to be found. This can perhaps be brought out better by a comparison of our results from tests at 15° and at 19° (Table I). It will be seen that this 4° difference in maintained incubation temperature results in a very pronounced difference in the amount of germination occurring within a given period of time after the first day or two.

MAINTAINED VERSUS FLUCTUATING TEMPERATURES

Many investigators have found that alternating or fluctuating temperature is more favorable for the germination of certain kinds of seed than maintained temperatures. Harrington ('23), who has reviewed the published reports of such work, lists 15 articles in which such conclusions are presented, and Morinaga ('26) has found that the same holds true for seeds of additional species. Such findings might well be expected, on some theoretical grounds, because germinating seeds are usually subjected to fluctuating temperature under natural conditions. Much seed testing has been done with the use of fluctuating temperatures, and Toumey and Stevens ('28) consider that a temperature fluctuation between 10° and 27° is most favorable for the germination of seeds of the greater number of coniferous species that have been tested.

It is to be noted in this connection that it is much more of a problem in technique to subject germinating seeds to maintained temperatures than to germinate them under conditions of fluctuating temperature, at least when rate of temperature fluctuation is not well controlled. Nevertheless, Nobbe ('90), Harrington ('23), and Morinaga ('26) have made comparative tests of maintained and alternating temperatures for the germination of seeds, and have found that maintained temperatures were at least as favorable as alternating temperatures with some kinds of seeds. Nobbe worked with forest-tree seeds and recommended a maintained temperature of 20° C. for testing seeds of *Picea vulgaris* Lk. and *Pinus sylvestris* L. Toumey ('16, p. 120) mentions a few other studies in which maintained temperatures were used in testing forest-tree seeds.

From the results in the present paper it is evident that some maintained temperatures were at least very satisfactory for the germination of the lodgepole pine seeds used. In nearly all of our tests 80 per cent of the seeds had germinated in 7 days at a maintained temperature of 24°, and in a few 90 per cent. Although we made no tests to compare maintained and fluctuating temperatures in relation to germination of lodgepole pine seed, a few preliminary tests with seeds of pitch pine (*Pinus rigida* Mill.) may be mentioned here. In these tests 100 dry seeds were planted on 10 cc. of 1-per-cent agar. Resulting germination percentages are as follows:

Temperature, degrees C.	Incubation period, days	Germination percentage
Alternating between 32° (10 hr.) and 11° (14 hr.)	5	11
	7	42
	8	69
Maintained at 32°	4	72
	7	82
Maintained at 10°	9	0
Maintained at 18°	4	0
	9	5

It appears that the 14 hours at 11° each day, to which the alternated seeds were subjected, was essentially wasted time, as far as promptness of germination is concerned.

Bates ('30) found better germination occurring in lodgepole-pine seed when it was subjected to a fluctuating temperature of 14°–26° C. (57°–78° F.) than when the temperature was maintained constant at 26°. For a 100-day incubation period, in sand, the germination percentages were 87 and 66, respectively; for his relatively short germination period of 20 days, the values were 59 and 3. The seeds for these experiments came from near Gunnison, Colorado, and 500 were used for each test.

In the case of both Bates's and Toumey and Stevens's studies we are dealing with temperatures which varied gradually through all intermediate temperatures between the maximum and minimum of the fluctuation. This

sort of temperature fluctuation may well act very differently from alternating temperatures like those of our pitch pine tests or those used by Korstian ('27) in his recent study of acorn germination. MacDougal ('14) has emphasized the probable significance of fluctuating temperatures in nature. With alternating temperatures the seeds are under the influence of maintained temperature most of the time, there being two different maintained temperatures; the periods of temperature change are very short and the changes themselves are correspondingly very rapid. With temperature fluctuation such as that described by Bates and by Toumey and Stevens, however, the temperature conditions cannot be easily depicted without resorting to graphs, for temperature change was more or less nearly continuous throughout the incubation period, its direction being reversed from time to time while its rate changed in various undescribed ways. The influence of maintained temperatures on biological processes is rather easily studied, and a knowledge of this kind of temperature relation should form a basis for the planning of useful experimentation on temperature fluctuation.

When experimentation on temperature fluctuation is to be undertaken, however, it needs to be borne in mind that two entirely new experimental variables must be introduced, namely: (1) the rate of change of temperature between maximum and minimum, and (2) the time relations of the temperature reversals. If two alternating, but in themselves maintained, temperatures are to be employed, the very short periods of temperature change may perhaps be neglected for first approximations, and the temperature conditions may be rather satisfactorily specified by stating the values of the two maintained temperatures and showing the time periods during which each of them is effective. In time relations of temperature reversals the number of experimental possibilities is very great, even in this simplest case; for the periods may be equal or unequal and of any length within the incubation period. Thus the maintained temperature might change regularly at 6-hour intervals, at 12-hour intervals, at 30-hour intervals, etc., or the change might occur after a shorter period at the lower temperature, and after a longer one at the higher, etc., etc. This suggests a complex but practically approachable problem with seed germination, for example.

When we turn to less restricted temperature fluctuation, however, the experimental problem becomes much more complex. It begins to resemble the problem of temperature influence in nature. Here the different maxima and minima may be respectively alike or they may differ markedly as the temperature swings upward and downward. The first maximum might be 25°, the second might be 30°, the third might be 18°, etc., and the series of minima might show this sort of variability also. The maxima and minima may occur at regular or irregular intervals, as in the preceding case, but periods of maintained temperature may not occur at all, or they may begin and end at any times, which would need to be specified. And finally, the gradual rate of temperature change between minimum and maximum, and

between maximum and minimum, will presumably be itself a variable during any given temperature swing, and the picture of this rate and its variations may not be the same for all upward swings or for all downward swings. For a downward swing it may not be at all like the reverse of the preceding upward swing. The complexity of the problem thus partially outlined, or at least suggested, is so very great that one would scarcely have the audacity to attack it excepting by the expression of mere opinion, hope, etc. It appears that the only promising way to approach this fundamental problem of fluctuating temperature and its influence on organisms is to begin by laying it aside temporarily, until much more shall have been learned about the influence of maintained temperature and alternating temperatures.

It is to be remembered of course that seed testing may have various objectives. In tests such as those described by Rafn, and by Toumey and Stevens, on the one hand, the purpose is to get an indication of the probable performance of a given lot of seeds when planted in the field or nursery. In such tests as ours, on the other hand, the object is an analysis of the underlying principles involved in seed germination. It may well be that in the former case some types of fluctuating temperatures may be hit upon, which may prove the more satisfactory. But in the present state of our knowledge of germination, there is a great need for further study of the influence of maintained temperatures.

Summary

In a brief series of germination tests made at 7 maintained temperatures (ranging from 15° to 41° C.) with seed of lodgepole pine (*Pinus contorta murrayana*) collected in 6 different localities in British Columbia, extending in altitude from 350 to 1,500 meters, it was found that the first germination occurred at the higher temperatures, in most cases at the highest employed, and that for certain periods of incubation there were two optimal temperatures for the occurrence of germination. These results corroborate earlier findings with seeds of several conifers.

The results of this study suggest that for a given species, seeds produced in colder climates may be expected to germinate more quickly at rather lower temperatures than those from warmer climates, and vice versa. This indication may lend support to the afforestation precept that there should be used only seed from climates very similar to that of the planting site.

The percentages of germination occurring in these tests for 7-day incubation periods at a number of temperatures are notably greater than those reported by some other writers. The temperature at which germination tests are made seem to deserve further consideration, including investigations of the effects of both fluctuating and maintained temperatures. Such studies should preferably be made with uniform moisture supply rather than the fluctuating supply used in many germination tests.

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REVIEWS

ENVIRONMENT OF THE PRAIRIE¹

This bulletin deals with that very extensive section of the United States known as the prairie. Botanically and agriculturally, it is a land area of great significance. Recognizing this fact long ago, the senior author set himself the task of understanding its environment (climatic and edaphic) in relation to the natural vegetation. As a consequence, he, together with his students, has gathered what is perhaps the most comprehensive and timely array of data respecting any major plant formation; timely because the original prairie conditions cannot be maintained, even now are fragmentary, and in another generation will have disappeared entirely. Ere the latter situation arose, Weaver and his co-workers have succeeded in determining the constitution and behavior of prairie vegetation with respect to the environmental complex (both above and below ground), and, in addition, established the important fact that this information is usable to a high degree in the solution of the problem of crop plant adaptation and culture.

The authors have submitted, in well summarized fashion, data on the environmental factors of unbroken upland and lowland prairie, which cover the growing seasons for a period of twelve years. After calculating the relative influence of the several factors (soil and air temperature, soil moisture, relative humidity, wind movement, and evaporating power of the air) they conclude that "water-content of soil and humidity are the master factors in the environment of the prairie. The climax vegetation is remarkably well adapted to these water relations." The effect of this authentic generalization should and no doubt will be that of encouraging all present efforts to increase, conserve and supplement soil moisture in crop cultivation, and to generate more and better research with that end in view.

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TWO BOOKS ON PLANT PHYSIOLOGY¹

For at least two decades the United States has had its share of competent plant physiologists. But their energies have been engrossed in laboratory

¹ Weaver, J. E., and Himmel, W. J. The environment of the prairie. *Conservation Department of the Conservation and Survey Division of the University of Nebraska, Bull.* 5, pp. 1-50, 16 figs., 1931.

¹ Maximov, N. A. A textbook of plant physiology. Translated from the Russian Edited by A. E. Murneck and R. B. Harvey. Pp. xvi + 381. *New York, McGraw-Hill*, 1930. Price \$4.00.

Miller, Edwin C. Plant physiology (with reference to the green plant). Pp. xxvi + 900. *New York, McGraw-Hill*, 1931. Price \$7.00.

and study, and with the giving of practical counsel in matters of applied biology. The result of this has been to delay the efflorescence into textbook form of a great deal of really good teaching. Of the present books, that of Miller is entirely a native product, while Maximov's work, with its two American editors, is decidedly sympathetic towards developments of the science in this country.

The short interval between the publication of these two books by the same commercial press suggests that there is a demand for texts ranging from elementary to encyclopedic. Miller's book is in the latter category—distinctly a learned treatise comparable with the best in other fields—yet readable and not in any way oppressive. A reference work *par excellence*, it will nevertheless prove useful for class purposes in many advanced courses.

It is a large book of 900 pages. The illustrations are well selected and well made. Tables are numerous. A good feature is the skilful description of important experimental methods. Useful and comprehensive questions are found at the end of each chapter.

Maximov's book is briefer, perhaps more casual, and designed for more elementary students. The author takes time to explain something, at least, about Donnan equilibrium and hydrogen-ion concentration. Statements are not documented, although numerous investigators are mentioned, all of which is as it should be. On the whole the exposition is lucid and worthy of the tradition set by Timiriazeff in his lectures to the laity. One may find places like the paragraph on stratification (p. 294) where more editorial finesse might have been used. On page 353 one learns that the pollen intine is "stretched into a long tube, which descends through the style." In general however, it would seem that the strictures of an earlier review² have been unduly severe.

To this reviewer a most interesting fact about both books is their effort to develop interpretations that will apply in the field. In other words, both books are *en rapport* with the ecological point of view. This is perhaps to be expected. Neither author has limited his own investigations to the indoor laboratory, and both have worked under conditions which were a constant reminder of the importance of making applications.

From the viewpoint of pure physiology, one must contemplate the titles of both books with a mixture of feelings. Approximately one-fourth of the smaller book is devoted to growth, movement, and reproduction. About one-half of that proportion in the larger book deals with growth. The remainder of both books is given over to a discussion of the physico-chemical processes of the plant. Of course we know most about the latter, and we are committed to the belief that only through them can the more intimate and complex characteristics of the living plant be explained.

But is such a commitment entirely good science? Where would organic

² Peirce, G. J. *Science*, 73: 422. 1931.

chemistry be today if it had paused until such time as physics and inorganic chemistry had supplied it with "fundamental" explanations upon which to proceed? After all, description of phenomena is the first task of science, and the issue of dealing with functions more profound than metabolism and plant physics is not to be met by the plea that we can only treat them empirically at present.

If the plant physiologist continues long to relegate such matters as individuality, development, response, to a more convenient future he may presently awaken to find them neatly tethered in another's pasture.

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DEFINITION AND DISCUSSION OF LIMNOLOGICAL TERMS¹

Limnology is a relatively new science, but it has shown a rapid growth during the past decade or two. Investigations in this field of science have involved geological, physical, chemical and biological phases of the subject, and its newness has resulted in the development of new pieces of apparatus, new methods and technique and new terms to express the various limnological relationships that have been found. The literature in which these methods and terms have been described is very widely distributed, and Naumann has performed a very welcome service by assembling them in a single volume.

The book is much more than a simple terminology, since the various terms are not only well defined, but many of them are discussed at some length and illustrated with figures. Many references are given to the original literature and the original definitions of the terms are quoted in many cases.

A large proportion of the terms refer to the ecological phases of limnology, so that the book is indispensable for those who are interested in freshwater ecology and in methods and apparatus for carrying on such studies.

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CONDENSED ACCOUNT OF SOIL MICROÖRGANISMS¹

"The Soil and the Microbe" presents in condensed form such essential facts in the life of soil microörganisms as their occurrence, function, and relationship to soil fertility. Detail which in Waksman's large reference book, "Principles of Soil Microbiology,"² filled 897 pages is here abbreviated to

¹ Naumann, Einar. *Limnologische Terminologie (Limnological Terminology)*. 776 pp., 158 figs. Berlin, Urban & Schwarzenberg, 1931. Price, paper cover RM. 46.40; bound RM. 50.00.

² Waksman, Selman A. and Starkey, Robert L. *The Soil and the Microbe*. New York, John Wiley & Sons.

³ Waksman, Selman, A. *Principles of Soil Microbiology*, Baltimore, Williams and Wilkins Co., 1928.
250 pages.

While the audience for which the book is intended is not stated, it appears to the reviewer that "The Soil and the Microbe" will be of most use to beginning students of soil biology and to scientists in closely related fields. With the exception of general citations at the end of the chapters, the authors have avoided the detailed references usually characteristic of scientific works. The use of complex equations and formulae, pp. 80-81, 126-129, and 163-164, the reviewer feels, may be of questionable value in this type of book.

The style of the book is readable, its type clear, and typographical errors relatively infrequent, although *percolation* on page 11, and microörganisms on page 157 are misspelled, while on page 104 *nitrite* appears for *nitrate*.

The graphs have been so reduced that it is not always easy to follow the lines. The tabular data do not always support the authors' contentions, as in the case of Table 27, page 123, where the figures from Giöbel are not primarily concerned with nitrogen fixation.

The book as a whole summarizes satisfactorily the most reliable work which has been done on soil organisms. It consequently fills a gap which has long been recognized and well deserves a place in the library of every worker in soil sciences.

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GAME SURVEY OF THE NORTH CENTRAL STATES ¹

The game survey which Aldo Leopold is carrying on under the Committee on the Protection and Restoration of Game of the Sporting Arms and Ammunition Manufacturer's Institute does not pretend to be a piece of ecological research. Yet it has a great deal of ecological significance and is of much interest to ecologists. For, the viewpoint of the author is ecological, and his book is a strong plea for ecological research in order to furnish a solid basis for game management. The theme which runs through the whole work is the influence of environmental conditions on game. Game must be considered as a crop, and conditions affecting game animals favorably or unfavorably must be studied just as they are in agricultural research. The efforts of game conservationists have hitherto been concentrated on bag limits and seasons, while practically no attention has been paid to the conditions which control the presence or absence of game. Bag limits are all very well, but will not furnish food and shelter.

"The survey concentrated on farm game because the crux of the problem is on the farm." The public wants the game, and expects the free run of

¹ Leopold, Aldo. Report on a game survey of the North Central States. 299 pp., 21 maps, 15 charts, 4 photographs, 58 tables. Madison, Wisconsin, 1931.

The report is distributed at cost, and may be obtained from the American Game Association, Investment Building, 15th and K Sts., N. W., Washington, D. C., at \$1.00 per copy.

the land, but offers the landowner no inducement for producing and protecting the game.

Modern farm practices, through clean culture, have reduced the game, notably bobwhite, by removing the cover. An example is given in 2 maps on page 27. The first map, in 1923, shows a 280 acre farm with 12 coveys of quail; the second, in 1929, shows where the ravines have been cleared and plowed, and the woodlot and brush land pastured. There were only 6 coveys in 1929, a reduction of 100 per cent. The author does not advocate a return to the former conditions, but the restoration of brush in waste and odd corners. He asks that the agricultural experts start experiments, and tell the farmers what particular measures can be taken to increase the game, and what response in game can be expected.

Grazing of woodlots, by destroying the young trees and underbrush, is ruining the farm woods as a habitat for game, especially for ruffed grouse. An important element in this situation is the diminishing use of wood for fuel and farm construction, and the consequent decrease in the value of the woodlot. "Sportsmen should realize that a wood-burning gas plant for farms, or even an efficient wood-burning furnace, would do more to keep woodlots, and hence grouse, on the map of rural America than many new laws or sermons on conservation."

The author recognizes the importance of fluctuations in animal numbers² and has a chapter on Game Cycles in the North Central States. Obviously, it was impossible for him to give much about the cause of the cycles because they are at present so little understood.

To the sportsman and to those interested in wild life, the report presents a picture of conditions, past and present, and suggestions for improvements, which are certain to have a far reaching influence on the public attitude toward game administration. The chapters on Game Administration, The Conservation Movement, and the Conclusions will be especially useful in this respect.

The report contains a great deal of information of interest to ecologists, but perhaps its greatest value, aside from its analysis of the present situation and constructive recommendations, is in pointing out the problems which need investigation. It literally bristles with questions which can be solved only by research, mostly by ecological methods. A good index increases the usefulness of the book.

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WASHINGTON, D. C.

² Elton, Charles. *Animal Ecology and Evolution*. London, Oxford University Press, 1930.

NOTES AND COMMENT

DEER CARRYING CAPACITY OF PENNSYLVANIA WOODLAND

It is obvious that the deer carrying capacity of forests differs greatly with the season of the year: thus a given area will support many more deer during the summer than during the winter; the fall is the time of greatest abundance of food, especially after sharp frosts have brought down the leaves and acorns; and the late winter, being the time of greatest food shortage, is the limiting season in this relation.

In this sense, therefore, the deer-carrying capacity of forests can be determined in the most significant manner during the winter, and must vary enormously with the character of the vegetation. It is equally clear that practicable determinations of the deer carrying capacity must be largely of the nature of estimates, subject to extensive factors of uncertainty.

The following quotations from an article by Henry E. Clepper¹ give several estimates of the deer-carrying capacity of forests:

"In some sections of France forest officers attempt to maintain a herd not to exceed 10 roe deer on one of their smallest administrative units of about 250 acres. In other parts of Europe attempts have been made to limit the deer population to one deer for each 40 to 50 acres. Early German foresters considered 8 to 16 adult red deer, not counting young, should be the limit for 2,500 acres. In Bohemia 15 to 35 head of red deer could be supported by 2,500 acres, but any addition would result in overstocking. European experience considered one red deer the equal of 2 fallow deer or 4 roe deer."

"Dr. C. A. Schenck advocated limiting the number of deer in the Southern Appalachian forests to 150 Virginia deer to 10,000 acres, or one deer to each 66 acres. Another writer states that in Northern Michigan 750 acres are capable of supporting 100 deer in good condition the year round."

"It may be concluded that of the thirteen million acres, constituting the total forest area in the State, only ten million acres support deer. If this estimate be granted, then we come to the rather startling observation that on an average there is one deer to every 12.5 acres of deer-supporting forest."

"With an average carrying capacity of 25 deer to each 1,000 acres on the ten million acres of deer-range, we find that the forests of Pennsylvania should have a deer population not to exceed approximately 250,000."

"It may be added to the above that while the estimate of the present number of deer in Pennsylvania's forests is necessarily highly unreliable, the lowest estimate made by intelligent observers is 800,000 deer as the present number in the State. This last and lowest estimate is from the bulletin quoted above."

This difficult problem, therefore, which can not be solved with directness and accuracy, must be attacked from all possible angles, in order to throw upon it the greatest amount of light.

The present study was suggested by an opportunity to observe 4 yearling deer which were confined in a woodland inclosure of 4.87 acres at the Pennsylvania State College through the spring, summer, and fall of the year 1930;² and inasmuch as the vegetation in this inclosure represented, in a general way, the optimum conditions existing in the state, the following observations may be considered to represent the upper limit of the very wide range of variation in the capacity of forests to support deer.

The woodlot in which the deer were confined is situated on Hagerstown soil of fairly

¹ Clepper, Henry E. The deer problem in the forests of Pennsylvania, *Bull. Dept. Forests and Waters, Pennsylvania*, 1931.

² Forbes, E. B., and Bechdel, S. I. Mountain laurel and rhododendron as foods for the white tail deer. *Ecology*, 12: 323-333, 1930.

high fertility. This is a residual Trenton limestone soil of the best agricultural type, which contributes but little to the deer-browsing area of the State, the latter being largely of De Kalb soil, which is of shale and sandstone origin, and which is the poorest type of land, from an agricultural point of view, in the state.

This woodlot is of gently rolling contour, and on 2 sides adjoins apple orchard. It is significant regarding the drouth-resistant character of the Hagerstown soil, that during the unprecedentedly dry season of these observations the adjacent orchards produced an unusually abundant crop of apples.

The 4 deer were approximately one year old at the beginning of these observations. They were turned into this lot on May 15, and continued there without other feed than that which they gathered for themselves until September 10, by which date the last available green leaf had been consumed, and the deer were living on twigs, acorns, and dry leaves. Even under these conditions of deficient food supply the deer seemed not to be eating the grass, a sparse growth of which was present. It is true that the browse was not completely exhausted, but the deer were in a poorly nourished condition, and the remaining feed was clearly insufficient to carry them through the winter.

From this time until the deer were taken away at the end of October, they were fed whole shelled corn and pea-size oil cake, which they like very well.

At the time the grain feeding was commenced the deer had not yet completed the shedding of their summer coats of hair; but almost at once after the grain feeding began they finished shedding.

After the deer were put onto grain feed they improved rapidly in condition, and came every day for their feed until the first frost brought down the main part of the season's crop of leaves, which had been beyond their reach. At this time they exhibited a marked falling off of interest in grain.

This area of 4.87 acres of woodland browse, of much better than average quality for the state, therefore, was insufficient to support 4 deer during their second year. This low capacity of even rich woodland vegetation to maintain deer is understandable in the light of the facts: (1) that a large part of the product of the forest is wood; (2) that the greater part of the leaves are out of reach during the growing season, and that the twigs of the taller growth are permanently out of reach; (3) that the fallen leaves soon lose their acceptability as food; and (4) that deer do not utilize grass nearly as thoroughly as do grazing farm animals.

Observations as to species of plants browsed by the deer were made in October. At this time there was no available green browse in the enclosure, and it was necessary to confine observations to the unbrowsed area surrounding the enclosure on all sides. Since the enclosure was in the center of a tract of considerably larger size, it is evident that the vegetation outside the enclosure was essentially the same as that on the inside.

The vegetation was of the type usually characteristic of mixed oak forests on the better types of soils, in which the dominant trees are *Quercus velutina*, *Q. rubra*, and one or more species of *Carya*, with smaller amounts of *Cornus florida*, *Fraxinus americana*, *Quercus alba*, *Prunus serotina*, and *Sassafras variifolium*. The under shrubs were largely species of *Cornus*, *Ceanothus*, *Corylus*, *Crataegus*, and *Vaccinium stamineum*.

The following plants, listed in order of their abundance, probably formed 75 per cent or more of the available browse for the deer: dogwood (*Cornus alternifolia*), Jersey tea (*Ceanothus americanus*), hazelnut (*Corylus americana*), deerberry (*Vaccinium stamineum*), sassafras (*Sassafras variifolium*), the wild cherries (*Prunus avium*, *P. serotina*, and *P. virginiana*), wild strawberry (*Fragaria virginiana*), broad-leaved aster (*Aster macrophylla*), oaks (*Quercus alba*, *Q. velutina*, and *Q. rubra*), hickories (*Carya spp.*), and loose strife (*Lysimachia quadrifolia*).

Certain additional species, probably of minor importance, belong only to the spring vegetation, and by October such plants had been so long dead that they would not be readily detected.

The above list of species is by no means complete for the area. One or more species of such representative genera as *Agrimonia*, *Antennaria*, *Apocynum*, *Cimicifuga*, *Daucus*, *Geum*, *Prenanthes*, *Polygonatum*, *Pteris*, *Rubus*, *Smilacina*, *Smilax*, *Solidago*, and *Veronica* were also noted, and other species and genera could be added.

It is evident, therefore, that this area supports a richer vegetation, both in number of species and in number of individuals, than do most areas of similar size and canopy in the surrounding mountains. Only on the less wooded ridges where the blueberries and sweet fern are common, or along the streams where ferns, sedges, and grasses grow in abundance, are areas comparable to this to be found. Moreover, our wild lands are grazed perennially so that the more palatable undershrubs do not in any one season produce the amount of browse present on the shrubs in the experimental area where there was no previous grazing.

CONCLUSION

These observations indicate that the area required to support a deer varies from a minimum of perhaps one acre of the best of forest browse, during the growing season, to a large and indefinite number of acres of sparser browse during the winter.

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SEASONAL DESTRUCTION OF A CTENOPHORE, *BEROE*, IN BARNEGAT BAY, NEW JERSEY

Although the fact was not known by Mayor and some other students of the Ctenophora, one of these forms, a *Beroe*, is a part-time resident of Barnegat Bay, New Jersey, being present in the bay in the summer two years out of every three, sometimes very abundantly, sometimes in small numbers. In winter it is entirely absent from Barnegat Bay; and, as it has no dormant eggs or larval stages, the supply, when present, must come each year from the sea outside. Probably it is borne by the Gulf Stream and southwest winds, carried near the beach by the compensatory bottom current caused by the overturn of water under an off shore or north to westerly wind, and sucked into the Bay at this time by the flood tides that occur twice each day.

The following note was suggested by an experience of the writer on Barnegat Bay in October 1925, when he was so fortunate as to be present at the critical time during which the entire colony of millions of these organisms were killed within a period of not more than 36 hours. The method of their removal was very plainly apparent. The incident will be described first, and followed by the discussion and conclusions.

During the early part of the week beginning Sunday, October 4th, 1925, Dr. Thurlow Nelson of the Zoological Department of Rutgers University mentioned to the writer that Barnegat Bay was particularly densely populated by *Beroe*, and it was decided to make a trip to secure some. The weather had been very fine and warmer than usual. The trip was planned for Saturday and Sunday, October 10th and 11th.

The trip to the Bay was made during the middle of the day on Saturday, October 10th. A cold clear northwest wind had arisen during the previous night, and increased during Saturday morning to a maximum of over 50 miles per hour around noon on the trip down. The air was cold, dropping from an average of over 60° F. on Friday to 32° F. on Saturday morning, and 36° F. on Saturday night. Arriving at Dr. Nelson's houseboat, the long narrow bay was seen to be whipped into foam with the waves, driven by the northwest wind, running from the mainland, or westerly shore of the bay to its eastern boundary, the barrier of sand that separated it from the ocean. It was too rough to fish for the *Beroe*, so that was given up until the next day.

Sunday morning, October 11th, a start was made in the motor boat, although the

TABLE I. Copy of the wind velocities and wind directions taken hourly by the U. S. Weather Bureau at Atlantic City, N. J., just below Barnegat Bay on October 9th, 10th, and 11th, 1925

Date 1925, October	A.M., hour ending												P.M., hour ending											
	I	2	3	4	5	6	7	8	9	10	11	Noon	I	2	3	4	5	6	7	8	9	10	11	Mid't
Hourly wind velocity (miles)																								
9th.....	4	2	2	3	2	2	4	7	8	12	14	14	16	12	11	14	14	15	21	22	18	18	15	25
10th.....	30	34	33	31	26	28	32	38	41	38	41	43	44	40	39	36	33	33	30	29	27	26	24	28
11th.....	21	22	22	20	23	23	25	26	26	26	28	26	23	21	18	18	17	14	13	14	14	14	13	
Maximum hourly wind velocity when it exceeds 32 miles																								
9th.....	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	36
10th.....	35	36	38	35	—	33	36	47	44	46	51	47	—	46	52	43	40	36	—	35	—	33	—	—
11th.....	—	—	—	—	—	—	—	—	—	—	None	—	—	—	—	—	—	—	—	—	—	—	—	—
Prevailing hourly wind direction																								
9th.....	SW	SW	SW	SW	SW	SW	SW	SW	SE	SE	SE	SE	SE	SW	SW	SW	W	W	W	NW	NW	W	NW	W
10th.....	NW	NW	NW	NW	NW	NW	NW	NW	NW	NW	NW	NW	NW	NW	NW	NW	NW	NW	NW	NW	NW	NW	NW	NW
11th.....	W	W	W	W	W	W	W	W	W	W	W	W	W	W	W	W	W	W	W	W	W	W	W	W

TABLE II. Copy of the air temperatures in degrees F., taken by the U. S. Weather Bureau at Atlantic City, N. J., just below Barnegat Bay on October 9th, 10th, and 11th, 1925

Date	A.M.												P.M.												Mean										
												Noon																							
	I	2	3	4	5	6	7	8	9	10	11	I	2	3	4	5	6	7	8	9	10	11	Mid't												
Oct. 9.....	56	56	55	55	54	55	57	62	64	63	62	62	61	60	60	60	59	57	54	52	50	49	45	54											
10.....	44	43	42	40	39	37	38	38	38	39	40	42	43	45	45	45	44	41	40	39	39	38	37	41											
11.....	36	36	35	34	34	34	36	40	43	46	48	50	52	53	55	55	52	51	50	49	48	48	44	44											

wind, still blowing on an average of 26 miles an hour, had hauled more west than northwest, and the temperature of the air was but slightly warmer, being only 39°.

Fishing with meter tow-nets of cheesecloth was undertaken during the morning hours from 9 A.M. to about 12 noon, but only a few *Ctenophora*, mostly *Mnemiopsis* and 3 very small *Beroe*, were taken, not over 12 in all during 3 hours towing. Those taken were found rather deep, near the bottom, in 5 to 7 feet of water toward the westerly edge of the bay.

After 12 M. it was decided to run the boat up on the west shore of the bay in the lee of the low marsh grass bank to eat lunch. Here it was found that the slight tide of the bay was about at ebb, and, in addition to that, this ebb was very much lower than usual owing to the strong northwest and west wind having forced so much water out of the bay during the preceding day and night. This difference due to the wind amounted to over 2 feet. A shallow slope of mud extended from the marsh grass bank down to and out under the water. The wind coming over the bank did not strike the water for several yards from the water line which was quite still.

Here, lying in the water near its edge, or stranded on the narrow mud bank by the falling tide, were literally countless fine specimens of *Beroe*, those on the mud bank freshly dead, those still in the water paralyzed or only using their comb plates feebly. They were mostly of large or medium size, and these masses and windrows extended up and down the west shore of the bay as far as the eye could reach. Later the boat was pushed off and visits made to other points on this west shore, and it was realized that almost the whole bay population of *Beroe* lay before us, stretched evenly along the approximately 30,000 yards of beach that bounds Barneget Bay on the west. Some were still in the water; most were stranded.

At a rough but fair estimate there were 25 individuals for each linear foot of beach, thus indicating a summer population of 2,250,000 *Beroe* in the bay. To this it would be fair to add 250,000 individuals that had not yet drifted into sight, making 2,500,000 in all.

The history of this movement and destruction was not hard to reconstruct with the aid of the Weather Bureau's records of wind direction and velocity (Table I), as well as air temperature (Table II), and also Dr. Nelson's water temperature and water level records (Table III and Fig. 1). On Friday, October 9th, and before, the temperature of the bay water up to 6 P.M. was 59° F. the air temperature 64° F. (Table III), and the *Beroe* were rather evenly scattered through the water of the whole bay, swimming leisurely in all directions and at all levels in pursuit of their food. Friday night at about midnight the wind came around from the northwest and began to blow at 25 miles per hour (Table I). The air temperature fell from around 60° F. to 45° and on Saturday

TABLE III. Bay water temperatures recorded by Dr. Nelson's self recording thermometer at the drawbridge at Island Heights. Maxima and minima for October 6th, 7th, 8th and 9th, and two hourly record for October 10th and 11th, covering the heavy wind and the extinction of the *Beroes*.

Monday, October 5th				Tuesday, October 6th				Wednesday, October 7th				
Maximum 61 F.				Maximum 59				Maximum 58				
Minimum 58				Minimum 56 .				Minimum 56				
Thursday, October 8th				Friday, October 9th								
Maximum 58				Maximum 58								
Minimum 56				Midnight—Minimum 55								
Sat. Oct. 10	2 a.m.	4 a.m.	6 a.m.	8 a.m.	10 a.m.	12 m.	2 p.m.	4 p.m.	6 p.m.	8 p.m.	10 p.m.	12 m.
	54	53	51	50	50	50	49	49	48	47	43	43
Sun. Oct. 11	2 a.m.	4 a.m.	6 a.m.	8 a.m.	10 a.m.	12 m.	2 p.m.	4 p.m.	6 p.m.	8 p.m.	10 p.m.	12 m.
	43.	44	42	42	40	39	42	45	46	45	46	46

morning it was around 38 (Table II), the wind velocity was 35 miles per hour, and the temperature of the water had fallen to 44° F., steadily lowering by its contact with this hard cold northwest wind, until on Sunday the water temperature was only 39° F. (Table III), a remarkable change only possible in so shallow a body of water.

When the water temperature fell on Friday night, and especially on Saturday, the *Beroe* were numbed, and, as a result of this and the violent disturbance of the surface waters of the bay, they sank as ctenophores always do under these circumstances to near the bottom so as to avoid cold and severe agitation.

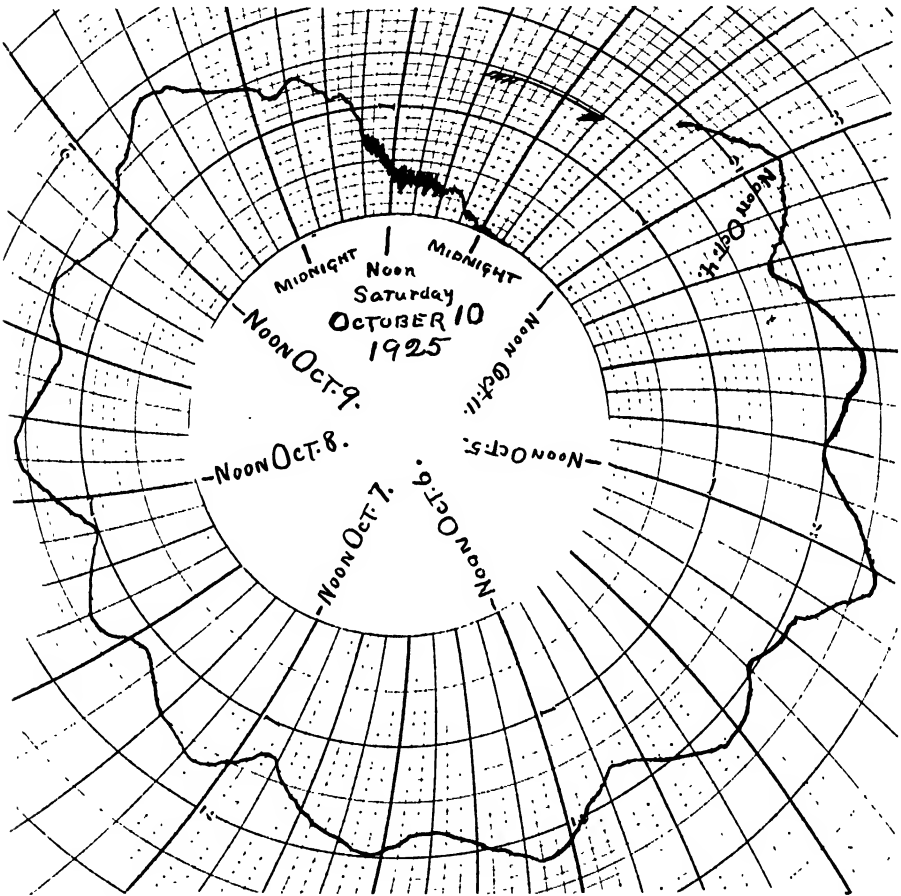


FIG. 1. Seven day record of the water levels from Sunday October 4th to Saturday at midnight of the 11th of October 1925; from Dr. Thurlow Nelson's automatic tide gauge at the drawbridge near Island Heights, New Jersey. The broad marking at the end of the line indicates the seiches set up by wind.

Meanwhile the strong winds had been driving the surface water of the bay from west to east. Some of this water was driven out of the narrow inlet, but the principal compensatory movement was of the bottom waters in the opposite direction (Fig. 2), carrying the numbed but feebly swimming *Beroe* toward the western shore where they came into contact with the mud bank and were stranded, or about to be stranded, some

time on Saturday by the falling morning tide together with the extra fall of water occasioned by the wind.

Two points arose in regard to how the overturn of bay water could not only bring the *Beroë* over to the western and windward side of the bay but also could bring them up so close to the beach as to strand them and still not carry them back over their course in the eastward current running on the surface. I am assuming that *Beroë* cannot orient itself with reference to the warmth and stillness of the water edge under the bank, and that the region of turning of the current extends from the water's edge out for some distance: a distance that would reach to greater depths than those in which the *Ctenophores* would strand.

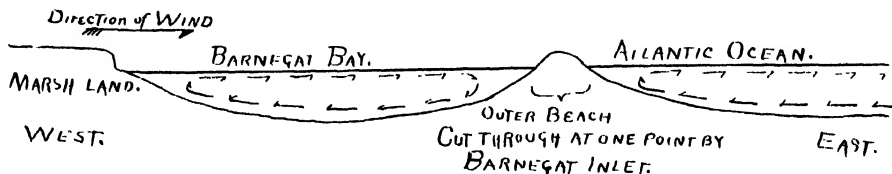


FIG. 2. Diagrammatic vertical section of Barnegat in west to east direction, with marsh bounding it on west and sand beach on east. Direction of wind and overturn of water caused by this wind indicated by arrows.

Thus, there is no doubt that a large number of *Beroë* would make the turn back to the east with the wind-driven upper current. But it is equally clear that the cold and the disturbance of this upper water would cause them to sink again, and, after only a short course they would find themselves once again in the stiller and warmer counter current moving to windward toward the bank (Fig. 2). This would form a zone of segregation a short distance out (about 4 feet) from the water line.

Assuming that they could not orient themselves with reference to the bank, but that they were all in slow motion in all directions (and the direction of motion of a *Ctenophore* is usually in a nearly straight line for several inches or feet), we would have to conclude that about one half of this segregated population would have swum into a stranding position in a period of time equal to that necessary for their average speed to carry them from the middle of the segregation area to water of a depth less than their diameter. Here the falling tide would quickly strand them. Meanwhile another segregated group composed of those which had moved out, sunk and been returned, plus newcomers arriving, would be constantly contributing to the number of the stranded and in the course of one six hour tide it seems that at least over three fourths of the population had become so stranded.

The bay is shallow, not over 6 feet on an average with some deeper channels, and it is proposed to take exact wind-water measurements of the currents during a northwest wind. Another paper on these currents, also on the wind-water movements which result in populating the bay with *Beroë* on most summers, is being prepared. There is some difference of opinion as to the species, whether this form is *Beroë cucumis* or *Beroë ovata*, which will also be studied and decided. The writer wishes to thank Dr. Thurlow Nelson and the U. S. Weather Bureau for data invaluable to this work.

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